Volume 28
Number 351 *Investigations in seed classification by family characteristics*
Article 1

July 1947

Investigations in seed classification by family characteristics

Duane Isely
Iowa State College

July, 1947 Research Bulletin 351

Investigations in Seed Classification by Family Characteristics

By Duane Isely

AGRICULTURAL EXPERIMENT STATION
IOWA STATE COLLEGE OF AGRICULTURE
AND MECHANIC ARTS

BOTANY AND PLANT PATHOLOGY SECTION

AMES, IOWA

CONTENTS

Investigations in Seed Classification by Family Characteristics[1]

By Duane Isely[2]

INTRODUCTION

The need to identify seeds may be encountered by individuals in several fields of biological endeavor. The greatest use of seed taxonomy in botanical and agronomic work is undoubtedly relative to seed analysis. One of the most important functions of the analyst is the recognition and designation of weed seeds occurring incidentally with agricultural seeds. The competent seed analyst must be able to recognize the seeds of a great many more or less common plants and should likewise possess the means of identifying, at least approximately, numerous less common ones. Application of seed taxonomy is not, however, confined solely to the realm of plant science. Zoologists, particularly those investigating the food habits of certain animals, must be equipped to do a certain amount of seed identification.

General seed morphology is closely allied with seed taxonomy, furnishing the groundwork of information by which seeds may be distinguished and classified. It would appear, in many cases, that structural characteristics will elucidate or verify the definition, position or relationships of various taxonomic categories; thus such characters would be of interest to the general systematist. Seed morphology, furthermore, has pertinent reference to seed physiology. To one making an inquiry into the germinative requirements of certain plant species, a knowledge of the structure of the seeds concerned is almost essential. The morphological nature of the seed, particularly that of the seed coat, frequently suggests the proper procedure in inducing seeds to germinate, or it may explain germinative peculiarities or behavior under varied conditions; differences in germinative behavior are frequently correlated with structural divergences.

Available literature on the subjects of seed classification and morphology is surprisingly small. The problem of seed identification is frequently a difficult one and considerably more involved than the identification of plants. It is true that one who has worked with seeds long enough to become familiar with a great many types can often approximately "place" an unknown on the basis of his experience. He can then, if possessed of a good working seed collection, verify his judgment and more precisely identify the seed by reference to the collection. The identification of seeds by one whose principal specialty lies

[1]Project 86 of the Iowa Agricultural Experiment Station.
[2]The plates were prepared by Mary Durrell, to whom the author renders thanks.

elsewhere poses a much more serious problem. There is neither any general all-over classification of seeds available nor any inclusive literature to which to turn. The individual, finding no orderly paths of procedure to follow in obtaining an identification, frequently decides that identification, even to family, is impossible.

In comparison, for plant identification one can turn to textbooks, manuals or monographic treatments which present classifications of the plants according to their various morphological characters. Such treatments frequently include analytical keys to families, genera and species which allow unknowns to be traced to their proper place in the classification scheme; verification can be obtained by descriptive and illustrative material.

There seems to be no good reason why a working classification of seeds cannot be achieved, on the basis of superficial and gross morphological characters, comparable to that in which plants are considered. This publication discusses certain important plant families from the standpoint of seed characteristics.

PERTINENT LITERATURE

General taxonomic literature relative to seeds is rather scanty. Certainly the most valuable contribution made in this country is the masterly series of drawings of weed seeds prepared by Hillman and Henry (7). These are issued in photostat form by the U.S.D.A. and have been duplicated, at least in part, in several other publications. They are the standard reference insofar as the identification of seeds by seed analysts is concerned. Korsmo (10) has prepared a somewhat similar reference work relative to European weed seeds. His plates are in color, and descriptions of the seeds are also included. In addition to the above-mentioned drawings, Hillman is the author of a pioneer contribution, "Testing Farm Seeds in the Home and in the Rural School" (6). This bulletin contains brief descriptions of the seeds of a number of weeds and crop plants in addition to illustrative material. Musil's more recent "Testing Farm Seeds in Home and School" (18) is similarly organized. Porter's general treatise "Testing the Quality of Seeds for Farm and Garden" (28) contains a section on seed identification. The Hillman-Henry plates are reproduced, and special emphasis is given to problems in differentiating seeds of similar appearance or close relationships.

As for studies of seeds in particular taxonomic groups, these have been made principally in a few families or genera where they have been accepted (contrary to the general rule) as essential if not the most important diagnostic structures. In the Cyperaceae and Umbelliferae, for example, the nature of the "seeds" (not true seeds in the strictly morphological sense) is relatively well known through treatment in the standard

manuals and monographic works. The value of seeds as diagnostic characters in miscellaneous families has likewise been indicated for a few genera (i. e., *Scirpus, Najas, Utricularia, Lycopus)* by various taxonomists, but there are relatively few papers dealing with genera or families primarily from the standpoint of seed characters. Among groups so treated, the following are prominent: The weedy and cultivated species of *Setaria, Panicum, Agropyron, Cuscuta, Brassica, Avena,* and *Poa* (Musil, 16, 17, 19, 20, 21, 22, 23), the Geraniaceae, Euphorbiaceae and Umbelliferae of Iowa (Murley, 13, 14, 15), "Akenes of Some Compositae" (Blake, 3).

Relative to the anatomical structure of seeds, Netolitsky (24) summarizes the literature up to 1926 and includes individual discussion of all families. Hayward (5) gives anatomical descriptions of the seeds of various economic plants.

TERMINOLOGY

One of the greatest barriers in intelligently describing the many variations found in seeds is the lack of a suitable descriptive terminology. Although I definitely feel the need for the development of a pertinent vocabulary in this field, I have deferred the coining of new terms; descriptions are for the most part carried out by using combinations of familiar morphological and taxonomic expressions. A few terms have, however, been used with restricted or modified connotation; the application of others has been avoided. Cognizance is taken of these below.

The word "seed" may be used in more than one sense. The morphological concept of a "seed" is well known and need not be more than briefly noted here. Seeds result from the continued development of ovules subsequent to fertilization; they are frequently defined as "matured ovules." A seed possesses an embryonic plant (uncommonly more than one embryo), stored food material which may or may not be incorporated within the embryo, and some kind of protective covering or coverings. The term "seed" may also be interpreted in a functional rather than in a strictly morphological sense. This is the usual interpretation in agricultural usage and is the one adopted here. Thus, the nutlet of the Mints, the mericarp of the Umbellifers, the achene of the Sedges, the carpel of the Mallows, the caryopsis or even floret of Grasses, and the true seed of the Legumes are all seeds in that they are embryo-containing, unit structures separating from the parent plant or its fruit and are potentially capable of developing into new individuals.

"Hilum" is applied in a more closely morphological connotation than seed. By "hilum" is meant the true hilum or funicular scar; functionally analogous areas on seed-like fruits are referred to as the "scar-area" or "scar."

The terms "elongate" and "compressed" are abundantly employed in the text. If not used with modifying adjectives, these refer only to a generalized condition; i. e., "elongate": an object which exhibits a greater extension in one dimension in proportion to the other two; "compressed": an object which is considerably shorter in one dimension than in the other two. No implication is given as to any other variations in form which such structures possess. A seed which is longitudinally elongate is lengthened parallel to the axis of attachment; one which is laterally elongate presents its greatest length at right angles to attachment axis. Thus in the former the hilum or scar would appear terminal at one of the ends; in the latter it would be laterally placed on one of the elongated margins or faces.

The adjective "sectoroid" is utilized in several instances. It refers to an object shaped like a section of an orange, i.e., with two converging plane faces and a curved dorsal one, sector-shaped in cross section.

Various authors in describing seeds frequently use the terms chalaza, micropyle, raphe and strophiole. Practical application of these expressions can be made by an individual who is distinguishing species within a given family in which similarity of superficial structures is such that one can define them in terms of gross morphological characters. Between unrelated groups, divergence of structural make-up and position is such that they are difficult to define by any means except in terms of developmental morphology. The scope of this paper is such that the use of the above-mentioned terms is of doubtful practical value, and they are applied as little as possible.

INTERNAL MORPHOLOGY OF SEEDS[3]

Attention has been given in this paper to certain gross internal characteristics of seeds in different families. These characteristics, described in detail under individual families, have to do primarily with the general form and position of the embryo, the presence or absence of a specialized reserve food tissue, and the position of this tissue relative to the embryo. The chemical nature of these structures is not discussed.

In the Monocotyledonous families (Gramineae and Cyperaceae) investigated in the present study, the bulk of the seed consists of reserve food tissue (endosperm). The embryo is basally placed, i. e., at the hilum end, and possesses a single cotyledon which is specialized as an absorptive organ and is in no way leaf-like in appearance. In general, the growing points, root and stem, are fairly well developed in the Gramineae and are usually rudimentary or in a very early stage of development in

[3]Notice has recently been received of the imminent appearance of an extensive paper concerning seed morphology by Dr. A. C. Martin.

the Cyperaceae. The embryo is generally relatively small, but may be somewhat elongate in some grasses.

In the Dicotyledons the embryo ranges in size from minute to large, occupying only a small portion of the seed cavity or entirely filling it. The cotyledons are two in number—occasionally reduced to one or absent in aberrant forms such as *Cuscuta*—and are more or less leaf-like in appearance. The radicle is usually well developed, the plumule commonly rudimentary.

The axis of the embryo may be straight or variously bent or curved. The radicle usually terminates at or near the hilum. It is characteristically otherwise in two common families, the Polygonaceae and Umbelliferae, in which the embryo appears turned over with the radicle uppermost or extended away from the hilum and the cotyledons downwardly directed. In the Polygonaceae this is due to the fact that the seeds arise from orthotropous ovules (those of most of our families are anatropous or campylotropous) and thus by comparison appear inverted; in the Umbelliferae, this is attributable to the fact that the "seeds" are one-seeded fruit-segments in which the seeds are pendent, thus upside down, from an apical placentation.

The cotyledons usually lie against one another (their ventral faces together), are thin and distinctly foliaceous or much thickened as specialized storage organs. They may be straight and flat, or curved either laterally or longitudinally, or both, are occasionally folded or convoluted, particularly in the Malvaceae and Convolvulaceae. In outline they range from oblong to broadly ovate or elliptic, are usually entire but may be notched or lobed.

A reserve food tissue external to the embryo is characteristic of many families, and remnants of the tissue are present in the seeds of nearly all flowering plants. This tissue is usually endosperm but in the Centrospermeae is chiefly perisperm, i. e., nucellar in origin, endosperm being absent or reduced to a thin sheath about the radicle. In families possessing a very small embryo, such as the Umbelliferae, the reserve food fills most of the seed. If the embryo is well developed, the food tissue is usually peripheral in position; contrariwise, however, in some groups with a curved embryo it may be both peripheral and central; in the Centrospermeae, it is almost entirely centrally located.

CLASSIFICATION OF SEEDS BY FAMILIES

Definition of plant families in terms of seed characters presents difficulties. This is to be expected. Elimination from consideration of all criteria except those exhibited by one set of structures (i. e., seeds) naturally makes the problem an exacting one. Nevertheless, the members of many plant families appear to exhibit tendencies in their seed structure which will allow relatively clear distinction from the representatives of other families.

The nature of the gross morphological structure of seeds, particularly embryo form and position, is of primary value in assigning their family relationships. While considerable literature (cf. Netolitsky, 24) is available upon the microscopic anatomy of seeds, relatively little, other than incidental notes in manuals, has been published relative to the comparative gross structure of seeds in various families. Gross internal morphology has still less been employed in a taxonomic sense, superficial characters having been relied upon almost entirely. This is perhaps one of the chief reasons for the non-development of any comprehensive classification allowing the identification of unknown seeds. A plant or flower which one knows can usually be recognized by external superficial characters; the same applies to many seeds. *Recognizing a known structure and identifying an unknown are, however, quite different processes.* If one wishes to identify an unknown plant in any of the standard manuals, he will soon find that external superficial structures alone will not suffice. In following a family key the ovary of the flower must be sectioned or dissected; the number of component locules, the number and frequently the position of the ovules must be observed. There is no reason to feel that identification of seeds should be easier—the converse is commonly true. It is essential that internal structure as well as external characteristics be given consideration if the study of seed taxonomy is to be given a definitive basis.

The nature of the general structural make-up of a seed can usually be ascertained by making cross sections in several planes and observing these under low magnification. If one has the skill, one can dissect out the embryo so that it can be observed entire. Seeds which have been soaked in water for a few hours are easier to work with than hard ones. Important characters which can be observed by such gross inspection include size, general form and orientation of the embryo, presence or absence of a specialized food reserve—if present, its abundance and position relative to the embryo—and the nature of the seed coat.

Superficial structures of seeds furnish valuable characters supplementing those of internal morphological nature. The general external alignment of the seeds is often very characteristic, e. g., whether elongated or compressed, rounded or angular, trigonous, sectoroid or of some other specialized shape. The position of the hilum, the aspect of markings, ornamentation of specialized structures possessed by the seed coat likewise are frequently diagnostic. The presence or absence (their nature if present) of associated structures (i. e., glumes of grasses) is commonly helpful. A number of families, e. g., Gramineae, Leguminosae, Compositae and Umbelliferae, possess seeds of rather characteristic appearance which can usually be easily recognized.

SCOPE OF THE PRESENT PAPER

Seventeen families are treated in this paper. These families are chosen from the viewpoint of the seed analyst, being those which appear to contain the greatest number of most important agricultural or weedy plants. Statements made concerning family characteristics have reference to plants occurring in this country, cultivated or wild, and may not be applicable to the family as a whole. While an attempt has been made to obtain as broad an outlook over these groups as possible, it is obvious that in a survey study of this kind many forms have been omitted; it is thus probable that certain exceptions can be pointed out to a considerable number of the generalizations given here.

A synopsis of family characteristics is given in the form of an analytical key. This key is based on seed structure as indicated both by external and internal characters. It has been prepared in a strictly artificial form in order to present distinctions in as concise form as possible; thus certain families, variable in morphology, will key out in more than one place.

The descriptive material for each family is prefaced by a short abstract of principal diagnostic characteristics to be used in recognizing that group. The more detailed discussion is divided into four principal parts headed "Morphology," "External Characteristics," "Associated Structures" and "Classification by Seed Characters," respectively. The first two items are self-explanatory by their title. The material under "Associated Structures" has particular reference to plant parts which are closely associated with the seeds, frequently persistent about them at maturity (i. e., grass glumes), therefore having diagnostic value. The nature of the pistil and fruit is also briefly described. The last portion, "Classification by Seed Characters," deals briefly with the utility of applying variations of seed structure within the particular family to subdivisions into tribes or other principal groups. Skeleton classification of subfamilies or tribes is presented in a few cases. Pertinent references are cited.

This summary is incomplete, both in coverage of all families and in treatment within the families. Present plans call for a continuation of this project. It is hoped, however, that the information presented in this paper will not only be of value in itself but will stimulate and point out a possible direction of inquiry for further investigations.

Dr. R. H. Porter, while director of the Iowa State College Seed Laboratory, reviewed the manuscript of this paper and made suggestions throughout the course of the work. The author hereby offers acknowledgment of this cooperation. Thanks are also due to Drs. W. C. Muenscher and O. L. Justice and to Mr. Charles Gilly for constructive suggestions.

FAMILY SYNOPSIS

1. Embryo with two (rarely one) leaf-like cotyledons.
   2. Cotyledons thin, laterally curved, folded or rolled up, usually also longitudinally folded or convoluted.
      3. Cotyledons laterally bent or curved, the curve at most scarcely exceeding 180 degrees; seeds subspheroid. *Cruciferae*
      3. Cotyledons laterally redoubled, folded or rolled; seeds various in shape, commonly irregularly sectoroid.
         4. Radicle-hypocotyl portion of embryo curved, extending nearly entire length of seed; seeds, if sectoroid, distinctly compressed, commonly persistent (mostly solitary) within a membranous pericarp covering; hilum frequently obscured by funicular remnants, with numerous fine lines radiating from a central hilar slit and presenting a grill-like appearance. *Malvaceae*
         4. Radicle-hypocotyl portion of embryo straight, relatively short; seeds, if sectoroid, irregularly turgid, mostly free from any pericarp association; hilum not as above. *Convolvulaceae*
   2. Cotyledons not folded or convoluted either laterally or longitudinally.
      5. Embryo longitudinally curved or bent.
         6. Embryo filling entire seed; endosperm absent or if present not discernible by gross inspection.
            7. Embryo spirally coiled. *Chenopodiaceae*
            7. Embryo not spirally coiled.
               8. Hilum inconspicuous, small, without a distinct margin, generally rounded, not laterally placed; seed coat roughened, usually punctate or reticulate, dull; radicle and cotyledons usually evident externally by distinct delimiting furrows; cotyledons placed edgewise or flatwise to radicle. *Cruciferae*
               8. Hilum frequently conspicuous, usually distinctly margined, round to elongate, commonly laterally placed; seed coat generally smooth and frequently shiny, rarely roughened or finely tuberculate; radicle-cotyledon position evident or non-evident; cotyledons placed edgewise to radicle. *Leguminosae*

6. Embryo not filling entire seed; nutritive tissue (usually endosperm) present, commonly abundant.
   9. Seeds three-angled or flattened, slightly elongate in face view and somewhat pointed at both ends; scar basal. *Polygonaceae*
   9. Seeds various in form, not three-angled or pointed; scar or hilum appearing marginal or lateral.
      10. Embryo peripheral in seed, curving around the centrally located nutritive tissue.
         11. Seeds roughened by variously ornamented cellular tuberculae—if nearly smooth, wing-margined; superficial cells wavy or sinuate-margined; seeds numerous in fruit (capsule). *Caryophyllaceae*
         11. Seeds smooth or nearly so, not tuberculate; epidermal cells not sinuate-margined; seeds solitary in fruit (utricle).
            12. Pericarp-covering at least partially persistent and adherent to seeds (usually greyish-cellular in appearance); seeds mostly dull black, commonly not rimmed. *Chenopodiaceae*
            12. Pericarp-covering not adherent to seed; seeds generally with a conspicuous rim, shiny black. *Amaranthaceae*
      10. Embryo not peripheral in seed; nutritive tissue external to embryo, or both external and internal relative to embryo position.
         13. Cotyledons narrow, scarcely broader than radicle; endosperm extensive, occupying center of seed as well as peripheral portion; seeds usually conspicuously flattened, frequently irregularly rounded in face view, mostly with a roughened or reticulate surface. *Solanaceae*
         13. Cotyledons conspicuously broader than radicle; endosperm scanty, peripheral; seeds usually not flattened, mostly with a nearly smooth surface. *Leguminosae*

5. Embryo straight.
   14. Nutritive tissue absent or not evident by gross inspection.
      15. Seeds (nutlets) mostly sectoroid in shape, the two plane (or somewhat convex) ventral surfaces meeting at right angles or less commonly curving together; scar usually clearly delimited, frequently very conspicuous at basal extremity of ventral angle. *Labiatae*

15. Seeds various; hilum or scar usually inconspicuous, not located as above.
    16. Seeds (achenes) elongate, usually longitudinally ribbed or smooth, sometimes cross-wrinkled or tuberculate; scar basal; apical extremity of seed pointed or depressed-truncate, frequently bearing capillary bristles or scale-like structures. *Compositae*
    16. Seeds or seed-like structures various, not as above described. *Rosaceae*
14. Nutritive tissue evident.
    17. Seeds (mericarps) plano-convex, or flattened, usually slightly elongate, mostly longitudinally ribbed (occasionally smooth or warty), borne in pairs with flat surfaces adjoined, frequently aromatic; scar scarcely discernible; embryo minute, difficult of observation. *Umbelliferae*
    17. Seeds various in shape, not longitudinally ribbed, borne within a dehiscent, dry fruit; hilum usually evident, frequently strongly conspicuous; embryo easily discernible.
        18. Hilum medial on seed face.
            19. Cotyledons only slightly broader than radicle; hilar face of seed frequently concave, or "scooped-out"; epidermal cells not sinuate-bordered. *Plantaginaceae*
            19. Cotyledons much broader than radicle; hilar face not concave; epidermal cells inconspicuously sinuate-bordered. *Caryophyllaceae* (Dianthus)
        18. Hilum basally or laterally oriented.
            20. Seeds with a narrow longitudinal suture extending entire length of surface; hilum commonly carunculate. *Euphorbiaceae*
            20. Seeds not possessing a longitudinal suture; hilum usually not carunculate.
                21. Cotyledons much broader than radicle; seed coat generally smooth; seeds not conspicuously small. *Leguminosae*
                21. Cotyledons only slightly broader than radicle; seed coat rough; seeds mostly minute, up to 2 mm. in length. *Solanaceae*

1. Embryo not possessing leaf-like cotyledons.
    22. Embryo filling most of seed, elongate, spirally coiled; seeds mostly subglobose, scarcely elongate. *Convolvulaceae* (Cuscuta)
    22. Endosperm filling most of seed; embryo usually small, not spirally curved; seeds frequently elongate.
        23. Embryo region discernible externally; seed (caryopsis)

various in form, usually not trigonous or compressed, generally enclosed by two to several persistent bract-like structures. *Gramineae*

23. Embryo not discernible externally; seed (achene) usually trigonous or compressed, generally free from associated glumes or enclosed in a sac-like structure. *Cyperaceae*

GRAMINEAE

(Plate 1)

GENERAL CHARACTERISTICS

The unit designated as the seed in this family most commonly consists of a one-seeded fruit, enclosed by two to several more or less closely adherent bracts. This structure is generally longitudinally elongate, sometimes much broadened and of a plano-convex form. Bracts usually two in number (lemma and palea), basally attached on each side of the seed. The seed (grain) proper is more or less elongate, smooth, minutely roughened or faintly striate on the surface. Endosperm abundant, filling most of seed cavity. Embryo basal, visible externally on the grain.

MORPHOLOGY

The grain (or caryopsis) is a one-seeded fruit developing from a superior, one-celled ovary possessing a single anatropous ovule. The ovule initially possesses two two-layered integuments which break down during maturation of the seed, the true seed coat ultimately being represented only by the persistent integumentary cuticula. Pericarp tissue is usually well developed, being reduced in only a few forms (e. g., *Sporobolus, Eleusine)* in which case the integuments assume a greater proportion of the protective function. Nucellar tissue is completely lacking or present as one-two rows of somewhat disorganized cells. The extensive storage tissue, endosperm, fills most of the seed proper. It is homogeneous in nature except for the outer one to two protein-bearing tiers of cells, the aleurone layer.

The embryo is basally located, lying against the side of the seed which faces the lemma in the spikelet. The axis of the embryo is, in general, straight and directed more or less parallel with the long axis of the seed, radicle downwards and plumule upwards. The single cotyledon (usually termed the scutellum) is a large, lateral structure which is attached at the first node of the seedling axis. It lies in direct contact with the endosperm, and upon germination serves to mobilize food reserves of this tissue for the embryo. The radicle is usually surrounded by a sheath-like structure, the coleorhiza. The plumule is commonly

well developed and is ensheathed by the modified first leaf, the coleoptile. The epiblast, a non-vascular structure arising from the main axis approximately at the level of the scutellum but opposed to it, is frequently present. The nature of this appendage is disputed.

EXTERNAL CHARACTERISTICS

The seeds are elongate longitudinally. In one of the planes parallel to the axis of elongation they are differentiated dorso-ventrally, in the other they are symmetrical. The embryo side of the seed is referred to as the dorsal surface; the opposing side toward the palea is the ventral surface. The lateral aspects may be distinct, or are more or less continuous with the dorsal.

The shape of the seed varies considerably. The grain may present its greatest thickness dorso-ventrally, i. e., compressed laterally, or may be flattened parallel to a dorso-ventral plane; it may vary from a narrowly oblong form to one in which the length scarcely exceeds the breadth; cross-sectional view may exhibit an elliptic, semi-circular or boat-shaped appearance. The most common form would appear to be a roughly ellipsoidal one, usually with the ventral face somewhat flattened, while the dorsal and lateral aspects are curved into one another. This alignment grades into another, particularly characteristic of several genera of the Panicum tribe, in which the seeds are plano-convex or "turtle-shaped." In many genera the ventral surface of the seed is longitudinally channeled or furrowed. The furrow may be evident only as a narrow seam, or may be both deep and wide so that the whole seed is markedly boat-shaped. The dorsal surface may be flat or convexly curved and more or less parallel with the curve of the furrow. This configuration is particularly characteristic of the Hordeae, but is by no means localized in this group, as various species of *Bromus, Festuca, Avena, Agrostis,* some species of *Poa* and others, present it to a greater or less degree.

The region circumscribed by the embryo is marked off externally on the dorsal side of the seed. This area, usually elliptic to oblong in outline, is frequently strongly furrowed, raised or lowered relative to the remainder of the surface. It is usually less than half the total length of the seed, but in some genera, i. e., *Zizania, Spartina, Pennisetum, Zea,* occasionally in *Echinochloa,* the embryo may extend from one-half to nearly the entire length of the grain. The scutellum is indicated by the upper and lateral portions of this area, while the embryo proper forms a ridge down the middle. The radicle is frequently somewhat extended beyond the base of the seed or divergently directed.

The scar area is basally located, opposing the embryo on the ventral side of the seed. It is frequently scarcely evident, but in some genera, particularly in the Panicum tribe, is strongly

marked as a rounded, reddish to black dot. The surface of the grain presents no very marked characteristics. It is usually smooth or longitudinally faintly striate.

ASSOCIATED STRUCTURES

The grain of most grasses is partially or completely covered by the persistent lemma and palea. As earlier indicated, common usage designates the "seed" as the grain plus these structures. In a few genera, e. g., *Sporobolus* and some species of *Eragrostis*, the grain at maturity readily separates from these accessory structures, but such forms are exceptions to the general tendency. In some crops, of course, one deals with the "naked grains" (wheat, rye, pearl millet), but in this case the grains have been artificially removed from their enveloping structures during the threshing process; weedy grasses associated with certain crops likewise may be threshed out along with the agronomic seed.

Grass flowers are borne in units known as spikelets; one spikelet may contain one to several flowers depending upon the particular grass to which it belongs. The spikelet is, morphologically, a shortened, ultimate stem branch bearing crowded, modified bract-like leaves, some of which subtend flowers. The lowest (or outermost) bracts of the spikelet are the "glumes" ("empty glumes" of some authors); these are two in number, are borne in close proximity to one another on opposite sides of the rhachis, and are never flower-bearing. In some genera one or both of these may be reduced or lacking. Subsequent glume-like structures subtend or may subtend flowers and are here referred to as "lemmas" ("flowering glumes" of some authors). The flower is borne at the apex of a short, secondary stalk in the axil of the lemma; it consists of a single pistil and ordinarily three stamens. The palea is an appendage of this secondary stalk, and is borne on the side opposing the lemma. The lemma, palea and flower form a more or less coherent unit which is termed the floret. At maturity, each floret may separate from the rest of the spikelet, or the entire spikelet may abscise below the glumes. The former alternative generally occurs in several-seeded spikelets, and the latter in one-seeded spikelets in which case the grain is more or less permanently enclosed within the glumes as well as the lemma and palea.

Variations on the above general scheme are manifold and offer the best characters for identification and classification of the members of this family. In some cases, several lemmas may be present but only one of them seed-bearing, the remainder being entirely empty or in some cases staminate. The position of these sterile lemmas relative to the flowering one is usually constant within a related group—e. g., in the Panicum tribe, the flower-bearing lemma is terminal and above a persistent sterile

one; members of the Phalaris tribe usually possess two empty lemmas below a terminal floret; some genera in the Festuca tribe possess empty lemmas, but these are above the perfect ones in the spikelet. The structure of the glumes, lemma and palea differs radically in different genera; they may be thin, membranous or papery, or contrariwise much thickened, leathery or chartaceous in nature. Usually one set of these structures forms a hardened protective covering about the grain, but the one which assumes this function varies in different groups. For example, in the Panicum tribe the lemma and the palea are greatly thickened and hardened, the empty lemma and glumes are thin and papery in texture. Conversely, in the Sorghum tribe, it is the outer glumes which are hardened, while the lemma and palea are very thin and membranous in nature.

Seeds of many grasses possess a short, basally attached, upwardly directed stalk or so-called "rhachilla." This structure is found in those groups possessing several-flowered spikelets, i. e., the Festuceae, Aveneae and Hordeae, and some of the Chlorideae. When the spikelet breaks up into the individual seeds, the main axis usually segments just below each floret, but the internode above the attachment of the floret is persistent as a basally attached stalk lying against the palea on the ventral side of the seed. Many members of the Andropogoneae possess two rhachilla-like structures. These appendages represent spikelet pedicels rather than a portion of a spikelet axis.

The lemma, palea and glumes are quite variable in shape and external markings, and are, in the main, responsible for the general appearance of the seeds. Their shape runs a gamut of forms ranging from those broadly rounded to others narrowly elongate with the tip much drawn out into a long bristle or awn. The lemma and glumes may be flat, laterally curved or sharply keeled. The palea is usually flat or concave; frequently it possesses a pair of low marginal keels. These structures are extremely various in the degree and nature of pubescence and nervation or ribbing.

CLASSIFICATION BASED ON SEED CHARACTERS

The principal taxonomic criteria used for classification of genera and tribes in this family have to do with number and arrangement of florets in the spikelets and the arrangement of the spikelets in the inflorescence. Since the grass "seed" consists of the matured floret, with or without associated glumes, characters exhibited by these structures may, likewise, be applied as a basis of seed classification in this family. On the basis of these and other existent variations in the structure of grass seeds, a relatively dependable segregation of many of our grasses is possible of achievement. No feasible classification of grains disassociated from their enveloping bracts can currently

be presented; determinations of such structures are frequently made only with considerable difficulty.

Musil has made very valuable contributions to our knowledge of the seeds of certain genera of this family. Genera discussed include *Agropyron, Setaria, Panicum, Poa, Avena* and certain miscellaneous forms (Musil, 17, 19, 20, 22, 23).

Seed characters of some of the principal tribes of this family follow:

Agrostideae (Typical genera: *Agrostis, Muhlenbergia, Sporobolus, Phleum.)* Spikelets one-seeded, with no sterile lemmas. Lemma, palea and glumes usually membranous—lemma hardened in *Aristida* and *Stipa.* Seed generally free from the glumes, consisting of grain surrounded by lemma and palea (soon free in *Sporobolus)* without a rhachilla but sometimes with a basal stalk or "callus." Grain mostly ellipsoidal or laterally flattened, commonly with a ventral suture.

Andropogoneae (Typical genera: *Andropogon, Sorghum, Sorghastrum, Erianthus.)* Spikelets one-seeded, a sterile lemma present below the fertile one. Lemma and palea hyaline-membranous; glumes thick and hardened. Seed usually consisting of the grain permanently invested by all of above-mentioned structures. Seeds commonly with a pair of basally attached, upwardly directed pedicels. Grain various.

Aveneae (Typical genera: *Avena, Danthonia, Holcus, Aira.)* Spikelets two to several seeded. Lemma and palea various, frequently hardened; glumes papery, as long as or exceeding spikelet. Florets separating at maturity into separate seeds or sometimes remaining attached. Rhachilla evident. Grain frequently grooved ventrally.

Chlorideae (Typical genera: *Chloris, Cynodon, Bouteloua, Eleusine.)* Spikelets one to several flowered. Seeds extremely varied, usually free from glumes, with or without an associated sterile lemma, with or without a rhachilla; agricultural seeds of the genera *Bouteloua* and *Chloris* frequently possess persistent, attached, sterile florets; those of the genus *Buchlöe* are clustered together in a bur-like structure.

Festuceae (Typical genera: *Festuca, Bromus, Poa, Glyceria.)* Spikelets several-flowered; glumes papery, lemma and palea likewise or somewhat hardened. Florets separating at maturity, seeds thus consisting of a grain within the lemma and palea. Rhachilla present. Grain ellipsoidal to oblong, commonly ventrally furrowed or channeled, sometimes very thin and boat-shaped.

Hordeae (Typical genera: *Triticum, Hordeum, Agropyron, Lolium.)* Seed characters same as for the Festuceae. These interrelated tribes are imperfectly distinguished on the basis of inflorescence characters.

Paniceae (Typical genera: *Panicum, Paspalum, Digitaria, Setaria.)* Spiklets one-seeded but with a sterile floret below the fertile one. Glumes papery, often much reduced; sterile lemma and palea usually papery or membranous; fertile lemma and palea indurate. All of these structures are more or less persistent about the grain.

Seed and grain frequently plano-convex in form. Rhachilla not present. Fertile lemma often distinctly marked or ornamented. Grain commonly with an evident darkened scar-area.

CYPERACEAE

(Plate 1)

GENERAL CHARACTERISTICS

Seeds (achenes) trigonous, lenticular or plano-convex; in face view varying from nearly equidimensional to narrowly elongate; usually rounded basally; pointed, beaked or possessing a swollen tubercle apically. Surface smooth or variously rugose, alveolate, reticulate or pitted. Achenes frequently in association with persistent subtending bracts or (in *Carex*) completely enclosed by a sac-like structure. Barbed bristles arising from base of the seed frequently present.

Storage tissue (endosperm) copious; embryo very small, basally placed.

MORPHOLOGY

The term seed, as commonly applied in this family, refers to a one-seeded fruit or achene; this structure consists of a single seed surrounded by a hard indehiscent pericarp. The seed develops from an anatropous ovule with two integuments.

The mature pericarp is frequently thick and very strongly developed, commonly possessing several distinct layers of thick-walled, heavily lignified stone cells. The seed coat, on the other hand, is greatly reduced, according to Netolitsky (24), being represented principally by the persistent cuticle. Abundant endosperm almost completely fills the interior of the seed. This tissue is starchy and whitish in color except for an external yellowish "oil-layer" which is readily observable by gross inspection.

The embryo is very small, basally located, and not readily discernible. Although somewhat varied in different genera, it usually consists of a laterally oriented loaf-shaped scutellum from the side of which arise the downwardly directed radicle and coleoptile. The scutellum is probably cotyledonary in nature, although complete agreement on this point has not been achieved. During the process of germination, it penetrates the endosperm and performs an absorptive and digestive function.

Schneider (32) and Wilczek (39) present a detailed analysis of achene and embryo structure in this family.

EXTERNAL CHARACTERISTICS

Although showing a wide range of variation in various superficial characters and attached appendages or associated structures, the seeds of the Cyperaceae are probably more constant in general form and appearance than in any other family of comparable size. The seeds are almost uniformly trigonous or compressed (plano-convex or bi-convex) and range from forms whose length only slightly exceeds the width to those considerably extended longitudinally. In outline they are most frequently more or less ovate or lanceolate, broadest at the base and narrowed toward the apex. The seeds may be basally rounded or cuneate, are sometimes short stipitate, or rarely with a swollen callus. The apex usually tapers to a point in an acute or acuminate fashion but is at times obtuse or rounded.

The apical beak characteristically possessed by the seeds of many species represents the persistent base of the style. In *Carex, Cyperus* and *Scirpus* a beak, if present, is usually continuous with the rest of the achene and of similar texture. In *Rhynchospora* and *Eleocharis,* however, it is clearly set off and variously differentiated. The beak, in the genus *Eleocharis,* is much swollen, producing the so-called "tubercle" which is not only helpfully diagnostic of the genus but variously characteristic for different species. A distinct tubercle is also present in *Rhynchospora* but differs in being much drawn out and pointed.

The basal scar is small, irregular and inevident. The surface ornamentation of the seeds of this family is extremely varied. It is smooth or microscopically roughened as in many species of *Carex* and *Scirpus;* smooth, finely alveolate or pitted to irregularly corrugated or wrinkled in *Cyperus;* in *Eleocharis* and *Rhynchospora* varies from smooth to alveolate or pitted, striate or rugose, sometimes variously irregularly ridged.

ASSOCIATED STRUCTURES

The presence of accessory associated structures greatly facilitates seed classification in this family.

Carex is definitely set off from other genera by the possession of the perigynium, a sac-like structure completely enveloping the achene. Not only is the presence of the perigynium diagnostic of the genus itself, but its variations in structure make it most useful in identifying the species within the genus. It is various in shape and nervation, hairy or glabrous, commonly apically beaked, with or without a two-toothed apex. Commonly the perigynium is closely enough adherent to the achene so that it

is persistent even in those seeds intermixed with crop seeds which have been subjected to various cleaning and threshing processes.

Cyperaceous flowers are subtended by membranous or scarious (occasionally foliaceous) bracts. These are sometimes persistent and remain attached at base of achene.

Slender bristle-like structures arising from the base of the achene are characteristic of certain genera. These are commonly inferred to be the remnants of a reduced perianth, hence are generally designated as perianth bristles. These structures may be smooth, finely barbed, or plumose; in length they approximate the achene or may be greatly elongated and exserted as in *Eriophorum* and certain species of *Scirpus*. They are characteristic of certain genera *(Scirpus, Eleocharis, Rhynchospora* and *Eriophorum* among the common ones), but all of these groups possess forms in which the bristles are completely absent.

CLASSIFICATION BY SEED CHARACTERS

The achenes and associated structures are of prime importance in the classification and identification of members of this family, hence have received more taxonomic attention than the seeds of many other families. Mackenzie (11) briefly describes and illustrates the perigynia, bracts and achenes of all North American species of *Carex;* Gale (4) and Svenson (35) have done the same for *Rhynchospora* and *Eleocharis,* respectively; McGivney (12) figures and describes the seeds of many species of *Cyperus;* Beetle (2) has prepared a key based upon achene characters to the North American species of the genus *Scirpus.* The more common genera of the Cyperaceae can be defined in an approximate fashion on the basis of seed characters. Usually the presence or absence of certain structures, namely the apical tubercle or beak, the perianth bristles and the perigynia, is most diagnostic; the character of the surface may in some cases be helpful. Specific identification is, in many cases, allowed by the manifold variations in the nature of these structures as well as that of the achene and the shape and nature of the subtending bracts.

The principal seed characters of certain important genera of the Cyperaceae are appended below:

Carex: Perigynium present. Achene usually nearly smooth, commonly short beaked. Perianth bristles not present.

Cyperus: Achenes variously roughened or nearly smooth, apically obtuse or short beaked. Perianth bristles absent.

Scirpus: Achenes usually nearly smooth, sometimes irregularly wrinkled, pointed but rarely apically beaked. Perianth bristles usually present.

Eleocharis: Achenes apically tuberculate, smooth or variously ornamented. Perianth bristles usually present.

Rhynchospora: Achene with an apical beaked tubercle, the surface variously roughened or ornamented.

POLYGONACEAE

(Plate 2)

GENERAL CHARACTERISTICS

Seeds (achenes) lenticular or trigonous, usually nearly smooth, mostly brownish or black, frequently partially enveloped by the persistent perianth. Endosperm present, usually copious. Embryo well developed, curved; radicle apically directed; cotyledons basal, flat or convolutely folded.

MORPHOLOGY

The ovary is one-celled and bears a single, basal, orthotropous ovule. The pericarp is hardened and indehiscent at maturity; hence the seed is a one-seeded fruit, an achene. The pistil may be either two- or three-carpellate, the former resulting in a lenticular fruit, the latter in a trigonous one. The integuments are two in number, or occasionally one, much reduced in the mature seed.

The endosperm is usually plentiful. The outer layer is specialized as a distinct external sheath and contains protein in contradistinction to the starchy nature of the rest of the endosperm. This layer is frequently referred to as the aleurone.

The embryo is longitudinally placed, bowed or nearly straight, with downwardly directed cotyledons and apical radicle. Its lateral orientation shows a certain amount of variation. In *Rumex* the position is against one of the sides of the seed, the cotyledons flatwise to the surface. In *Polygonum* the embryo is usually axial or marginal, following one of the corners or edges. Woodcock (40) reports that the embryo of *Eriogonum microthecum* is quite large, medial in position, and divides the endosperm into two separate segments.

The cotyledons are commonly narrow and thick as in many species of *Rumex* or they may be broad and relatively thin. They lie flatwise together and are usually straight laterally. In *Fagopyrum* these structures are broadly reniform, quite thin, and are convolutely folded or irregularly rolled in the seed.

EXTERNAL FORM

The seeds are almost uniformly trigonous or two-sided, mostly slightly longer than broad; the faces are ovate to ovate-lanceolate, basally rounded, apically pointed or somewhat acuminate. The edges are rounded or angled, almost wing-angled in some species of *Rumex*. The surface is smooth, frequently shining or faintly pitted or roughened, generally brownish or black.

ASSOCIATED STRUCTURES

The seed is commonly entirely enclosed within the persistent perianth, the five-six separate lobes of which slightly exceed the achene and surround it in a valvate or laterally imbricate fashion. Even if the major portion of this structure is destroyed, the closely adherent basal portion frequently remains attached, particularly in species of *Polygonum*.

CLASSIFICATION BY SEED CHARACTERS

It appears that most of our common genera of Polygonaceae can be distinguished by seed characteristics. Color, shape of the seed, position and form of the embryo are probably the most important items. Additional verification can be obtained if perianth structures are present. Identification of species within the genera may be more difficult inasmuch as the seeds of many are very similar; this is particularly true of *Rumex* achenes divested of their perianth covering.

CHENOPODIACEAE

(Plate 3)

GENERAL CHARACTERISTICS

Seeds compressed, lenticular to plano-convex; in face view circular to narrowly obovate; *Salsola* thickly obconic. Margin (or tip) interrupted by a small notch or beak. Surface smooth or minutely pitted, black to brown, shiny or dull, frequently partially or completely obscured by a cellular, scarious membrane (pericarp). Seeds mostly initially enclosed within the persistent calyx or floral bracts.

Embryo curved into a ring or assuming a horseshoe shape. Nutritive tissue (perisperm) usually present, occupying central portion of seed. In *Salsola* the embryo is spirally rolled up and nutritive tissue absent.

MORPHOLOGY

Ovules campylotropous to anatropous, usually with two integuments, solitary in the one-celled ovary from a basal or *(Beta)* marginal placenta. The pericarp is greatly reduced at maturity and although indehiscent is usually thin and easily scuffed off. This type of a one-seeded structure is defined as a utricle; thus the seeds are, until destruction of the pericarp covering, technically one-seeded fruits. The seed coat is usually well developed, one-two layered.

The internal gross morphology is typical of the Centrospermae (described in more detail under the Caryophyllaceae), and is characterized by a curved or spiral embryo usually surrounding a centrally placed nutritive material. The cotyledons of the

embryo are long and relatively narrow, usually thick. The nutritive material is perisperm; the endosperm is reduced to a thin sheath about the radicle. The perisperm is also greatly reduced in species having spiral embryos, or present in two small portions separated by convolutions of the embryo.

The seeds of our species can be divided into three arbitrary groups as regards the form of the embryo. These embryo types are: (1) Embryo *(Chenopodium, Atriplex)* ring-shaped or slightly exceeding a complete revolution of 360 degrees. The apices (cotyledon and radicle) may meet flush, the radicle may slightly overlap the terminus of the cotyledons, lying against the outer cotyledon, or it may be short and divergently projected. (2) Embryo *(Axyris, Bassia)* roughly horseshoe shaped, bent through a curve of 180 degrees, the ends acuminately curved together and meeting or lying parallel for a short distance. (3) Embryo *(Salsola)* spirally coiled through two or three revolutions.

EXTERNAL CHARACTERISTICS

Seeds compressed, orbicular to cuneate-obovate in lateral view, the surface generally plane to convex, sometimes centrally depressed; margins rounded or drawn out into an obtuse rim. *Salsola,* with its thick obconic form and lateral spiral furrows, is an exception to the above statements. In general, there is a fair correlation between the above-described embryo types and the seed shape. The circular embryo is characteristic of rounded seeds, the "horseshoe" embryos of elongate forms; the spiral embryo may be found in either obconic or (uncommonly in our species) rounded seeds.

The marginal notch is evident or scarcely discernible, in elongate seeds is located at the narrow end. A shallow superficial furrow directed toward the center of the seed may or may not be present.

The scar area on the outside of the fruit coat is various in position relative to the seed. It may be lateral in the middle of one of the faces, or marginal in the vicinity of, or opposing, the marginal notch. The lateral scar is characteristic of the so-called "horizontal" seeds which lie in the calyx with the flat sides dorso-ventral; the marginal scar is found in seeds which are "vertical" with the flat sides running up and down. Frequently, particularly in horizontal seeds, the pedicel breaks off below the remnants of the calyx so that the calyx base and a short irregular stalk are evident outside of the pericarp. The true hilum is at, or in the neighborhood of, the marginal notch and is very inconspicuous.

The pericarp forms a thin, scarious, semi-translucent covering through which the color of the seed coat underneath is dully observable. It is loosely adherent to the seed and can usually

be easily removed by abrasion. The constituent cells are commonly quite large and can be observed under low magnification. The remnants of the style base are frequently evident, particularly in "horizontal" seeds, on the side opposite the scar.

The seed coat is usually brown or black, commonly well developed and thick. The surface is smooth or minutely pitted, tubercular in *Salicornia.*

Some members of this family possess dimorphic or even trimorphic fruits. Genera in which this occurs include *Atriplex, Chenopodium* and *Axyris.* This variation in fruit structure within a single species includes slight differences in shape, variation in position (i. e., vertical or horizontal) and the presence of more than one color form.

ASSOCIATED STRUCTURES

The calyx, where well developed, is persistent and partially or completely surrounds the seeds. It usually consists of five greenish or membranous lobes which are superficially glabrous or hairy, sometimes mealy-granular, frequently variously keeled, winged or awned.

In the genus *Atriplex* the seeds are enclosed in a pair of close-fitting, foliaceous, valvate bracts. In *Spinacia* the same situation is present, but the bracts at maturity become much hardened and completely fused together so that the seed is contained in a small nut-like structure. Flowers in the genus *Beta* are borne in glomerules, the constituent calyces of which at maturity become irregularly corky-thickened and adnate to one another—the result is the several-seeded beet "seed-balls" of commerce.

CLASSIFICATION BY SEED CHARACTERS

The two principal subdivisions of the Chenopodiaceae may be designated by seed characters as follows:

Cyclolobeae. Embryo curved into a ring or horseshoe shape surrounding the centrally placed nutritive tissue. Examples: *Chenopodium, Atriplex, Bassia, Axyris.*

Spirolobeae. Embryo spirally coiled. Nutritive tissue absent or separated into two individual portions. Example: *Salsola, Sarcobatus, Suaeda.*

Individual genera may be, at least to some extent, identified by the shape, color and scar position of the individual utricles. Identification is, however, greatly facilitated if the calyx remains for observation. The calyx characters previously mentioned, as well as the position of the seed inside, frequently allow rather definite generic identification. For example, *Chenopodium* is characterized by either vertical or horizontal seeds nearly enclosed in the calyx, the lobes of which are flat or somewhat keeled, usually mealy or glandular. In *Cycloloma,* the calyx is laterally winged and seeds horizontal. *Bassia* possesses

horizontal seeds surrounded by a hairy and usually spine-tipped calyx. The *Corispermum* seed is erect, possesses a vertically winged pericarp; the calyx is much reduced or absent. Accessory structures, characteristic of the genera *Atriplex, Spinacia* and *Beta,* have already been discussed.

AMARANTHACEAE

(Plate 3)

Similar to Chenopodiaceae. In our species the seed is usually free from pericarp and calyx covering.

Of the few genera of this family represented in this country, *Amaranthus* is much the most common. The seeds are shiny black, lenticular, rounded or slightly elongate, with a distinct marginal rim. The various species are all very similar as to seed characters and hence difficult to differentiate. The seeds of *Acnida* are similar to those of *Amaranthus* (but pericarp indehiscent in *Acnida cannabina);* those of *Froelichia* are contained within the hairy calyx.

CARYOPHYLLACEAE

(Plate 3)

GENERAL CHARACTERISTICS

Seeds compressed, usually rather plump with thick margins; in face view irregularly rounded, subreniform to slightly elongate. Hilum marginal (except in *Dianthus),* in a shallow notch or flush. Surface generally rough or tuberculate. Embryo circular, curved about the margin of the seed, rarely nearly straight or spiral. Nutritive tissue (perisperm) copious, mostly centrally placed relative to embryo.

MORPHOLOGY

Ovules campylotropous to subanatropous, with two distinct, two-layered integuments.

The mature seed coat contains derivatives of both integuments. The epidermal layer is specialized in a characteristic manner which is rather specific for this family. The constituent cells are large, easily observed externally under low magnification, and possess wavy or toothed margins; the outer walls are much thickened, humped or raised into tuberculae or papillae-like structures.

The embryo possesses a well-developed radicle, hypocotyl and cotyledons. Its position and configuration is the principal factor in determining the characteristic shape of the seeds. Usually nearly cylindrical in cross-section, it lies about the margin of the seed, its length approaching the complete circumference, radicle and cotyledon apices terminating on opposing sides of the hilum. The cotyledons are usually thick and narrow, their

faces oriented parallel to the margin of the seed, i. e., flattening of the seed is edgewise to the cotyledons. In some genera, for instance *Agrostemma,* the cotyledons may be broader and flatter than the "typical" form. In this case the seeds in edgewise view appear quite thick and may be nearly equidimensional. A few variations in embryo position exist. Among those observed is that in the genus *Spergula* in which the embryo, possessing a length greater than the circumference of the seed, is spirally curled. The embryo configuration in the general *Dianthus* and *Tunica* is utterly unlike the characteristic form of the family. Here it is not curved but straight, possesses a short radicle and hypocotyl and large flattened cotyledons; the seed is compressed parallel to the face of the cotyledons rather than at right angles to them as in the rest of the family.

The abundant nutritive tissue characteristic of this family is not endosperm, as stated by many botanical manuals, but perisperm. For further information concerning origin of storage tissue in this and related families, see literature cited: Woodcock (41, 42), Artschwager (1), Netolitsky (24), and Pax and Hoffman (26). The perisperm is usually copious and occupies the central portion of the seed inside the embryo. Endosperm is reduced to a thin sheath about the radicle. The alignment of the embryo, the position and nature of the storage tissue, as above described, is typical not only of the Caryophyllaceae but the other families of the Centrospermae (Amaranthaceae, Chenopodiaceae et al.) and is the principal basis of the taxonomic classification which groups them together.

EXTERNAL CHARACTERISTICS

Seeds irregularly compressed to nearly equidimensional, in face view varying from nearly circular to subreniform or slightly elongate. Hilum marginal, in elongate seeds at the narrow end, in the reniform type lateral. It may be flush with edge of seed but is most commonly in a shallow notch or is confluent with a pair of radially directed short furrows, one on each face of the seed. The two shoulders of the notch or edges of the furrow indicate the space of divergence between the apices (cotyledon and radicle) of the embryo which approach one another but fail to meet in an even line.

The seed faces are not plane but variously slanted or curved; they are commonly concentrically concave toward the hilum; thus the seed is thinner at this end than distally. The edge or margin of the seed is usually convex and is not set off from the faces by a definite angle. Marginal wings are present in a few genera, for instance some species of *Lychnis* and *Spergula.*

The hilum usually consists of a circular or elliptical pit with no particular distinctive markings. Sometimes it is partially

or almost completely surrounded by a distinct raised collar or rounded ridge; in other cases, the ornamentation consists of a pair of lateral swollen prominences which partially block the hilar furrows or notch. Such structures are particularly well developed in *Silene noctiflora* and other members of this genus.

The seed surface is most commonly dark in color and is roughened or tuberculate. The superficial cells, previously discussed, are usually easily discernible externally; the typical sinuate margins can commonly be seen. The rough appearance of the surface is due to a humped-up appearance of the individual cells, or to the presence of cylindrical or pointed tubercles, one to each cell. The cells located on the faces are usually longitudinally elongated and pointed in the direction of the hilum. They may or may not be arranged in lateral concentric rows. The marginal cells are less distinctly elongate and are in definite longitudinal rows directed about the circumference. Those in the vicinity of the hilum are much smaller than on the rest of the seed and have a squeezed appearance. In some genera (i. e., *Spergularia)* the surface appears nearly smooth. In such cases delicate cylindrical or clavate papillae are initially present but are mostly lost on mature seeds.

The nature of the embryo of the genus *Dianthus* has already been noted. The external alignments of the seeds of this genus are likewise atypical. They are strongly compressed, but the plane of compression is against the hilar side rather than at right angles to it; the hilum is thus medially located on one of the faces and over the middle of the straight, flat cotyledons rather than between the tips of radicle and cotyledons. The radicle is slightly exerted at the narrow end of seed and is visible externally as a short, pointed protuberance. The relationship between this form and that exhibited by most members of the family is not clear.

ASSOCIATED STRUCTURES

The fruit of the Caryophyllaceae is a one-celled capsule bearing the seeds in free-central or basal fashion. Normally the seeds completely separate from this structure at maturity.

CLASSIFICATION BASED ON SEED CHARACTERS

Seeds have been little used for classification or identification of the members of the Caryophyllaceae. Those of many genera are so similar that a definition of genera in terms of seed characters scarcely seems feasible. Likewise the seeds of species within a genus are frequently much alike; some species in different genera may bear such striking resemblances that their separation is difficult—i. e., *Lychnis alba* and *Silene noctiflora;* thus the whole problem of specific identification within this family is rather involved.

Of the two tribes (or subfamilies if one prefers) making up the Caryophyllaceae, the seeds of the Alsinoideae tend to be quite small, vary from a slightly elongate form with the hilum at the end *(Cerastium)* to a lenticular configuration with hilum very evident *(Spergularia)*. The seeds of the Silenoideae average larger, are commonly subreniform with the hilum in a lateral notch, or are irregularly equidimensional.

CRUCIFERAE

(Plate 4)

GENERAL CHARACTERISTICS

Seeds elongate longitudinally, roughly ellipsoidal or obovoid to variously flattened, occasionally subspherical. Hilum inconspicuous, frequently obscured by adherent whitish funicular material. Seed surface mostly minutely roughened by fine pits, papillae or reticulations, occasionally coarsely reticulate or with curving ribs. Embryo filling seed cavity. Radicle long, usually strongly curved near point of origin and extending along the margin entire length of seed—frequently forming an external notch or lobe at terminus. Cotyledons usually flat, lying edgewise or flatwise to radicle, occasionally folded over or curled. Endosperm greatly reduced, not evident by gross inspection.

MORPHOLOGY

The ovules are campylotropous and possess two integuments.

The seed coat is several layered and contains derivatives from both integuments. The cells of the outer epidermis of the outer integument suffer partial dissolution; the lower portions of their lateral walls, however, are persistent and become thickened, suberized and variously sculptured. They are responsible for the characteristic finely roughed or reticulate appearance of the seeds of this family. The inner integument may at maturity be reduced to a membrane or may persist as a single or double layer of compressed, pigment-containing cells.

Aleurone tissue, a single layer of cells in thickness, lies within the seed coat; it generally is interpreted as being endosperm. Nucellus is absent in mature seeds.

As indicated above, the radicle is well developed and marginally placed in the seed. Its position relative to the cotyledons, however, is varied, likewise the configuration of the cotyledons themselves. Most commonly the cotyledons are flat and straight; both of them may be in contact with the radicle, the latter marginal, or the radicle may touch only one of them, lying against the flat side. The first position is termed accumbent; seeds of *Thlaspi, Alyssum, Berteroa, Arabis* and *Draba* characteristically exhibit this configuration. The flatwise placement

of the radicle relative to the cotyledons is referred to as an incumbent condition; characteristic genera are *Capsella, Sisymbrium* and *Conringia.* Members of the genus *Lepidium* exhibit both of the above described embryo forms. The cotyledons of accumbent embryos are usually thin, rather broad, commonly obovate in outline; the seeds with such embryos usually appear laterally compressed, the cotyledons lying parallel to the plane of flattening. Seeds possessing incumbent embryos, on the other hand, tend to be ellipsoidal or irregularly ovoid, commonly with a conspicuous radicle-ridge; the cotyledons are mostly thick, rather narrow, elliptic in outline; they may be parallel or obliquely placed relative to the external broad surfaces of the seed. A third embryo form is exemplified by *Brassica* and *Raphanus.* The radicle lies against the flat side of one of the cotyledons as in incumbent seeds, but the cotyledons are folded laterally about the radicle and are strongly notched apically; the seeds tend to be spheroid in appearance. In a few genera the cotyledons are recurved apically or spirally rolled up from apex to base. Wettstein (36) puts all members of this family having embryos of this nature in a separate group which he calls the Spirolobeae. The genus *Bunias* is an example.

EXTERNAL CHARACTERS

The principal general forms assumed by seeds of this family have been discussed above in connection with their morphology. The external appearance is strongly correlated with, or perhaps more properly determined by, embryo form. The position of the radicle is commonly distinctly marked externally, in accumbent seeds by a furrow running parallel to the margin of the seed (and set off from it the thickness of the radicle), in incumbent forms by a distinct ridge; the line of demarcation between the cotyledons is also frequently evident in such seeds. Radicle and cotyledon position are not strongly evident externally in the rounded (conduplicate) seeds of *Raphanus* and *Brassica* although the radicle may be partially evident as a low ridge.

The nature of the very characteristic finely roughened seed surface has already been indicated. In a few genera coarser markings are present, as for instance the numerous concentrically curving ridges in *Thlaspi* and the rough high reticulations of *Neslia.*

ASSOCIATED STRUCTURES

The fruit of this family is a two-celled pod-like structure known as a silique (longer than broad) or silicle (short and broad). In most genera it is dehiscent and the seeds are soon free, but in a few it becomes semi-woody and indehiscent. Examples are *Raphanus, Cakile* and *Chorispora.* Such fruits are

frequently variously constricted and break up into one-two seeded segments. Externally these indehiscent siliques, or fragments thereof, are hard, straw-colored to brown, longitudinally furrowed or striate, and appear much like dried-up stem fragments.

CLASSIFICATION BY SEED CHARACTERS

Seeds are used in some current taxonomic treatments of the Cruciferae to separate tribes and in defining some of the larger groups of this family. The validity of the use of seed characters for delimiting natural lines in this family depends on one's taxonomic viewpoint; in any case, they are useful in making convenient, albeit perhaps artificial, divisions of the family.

Among the species of single genus (or sometimes of several genera) differences between the seeds are frequently minute and inconsistent. Specific identification of some species of *Brassica*, for instance, is very difficult by seed characters; the same applies to *Sisymbrium*.

ROSACEAE

(Plate 5)

GENERAL CHARACTERISTICS

Family extremely difficult of definition in terms of seed characters because of varying degree of association of seeds with carpel and hypanthial structures. "Seed" a true seed, an achene, an achene (or achenes) surrounded by hypanthial material, or a nut-like structure ("stone") consisting of a seed and a portion of the pericarp. Shape and surface of these structures extremely diversified. True seeds commonly elongate with a terminal hilum and a longitudinal raphe-like ridge or suture.

Endosperm much reduced. Embryo straight with large, turgid cotyledons, and a short radicle.

MORPHOLOGY

Morphologically the "seeds" of the Rosaceae may be true seeds, e. g., *Spiraea, Malus;* they may be one-seeded fruits, achenes, e. g., *Fragaria, Potentilla, Rosa, Geum;* they may be achenes enclosed within a persistent, hardened hypanthium, e. g., *Sanguisorba, Alchemilla;* or they may include both seed and stony endocarp tissue, e. g., the stone of *Prunus* fruits.

The ovules are more or less anatropous; integuments may be one or two.

The seed coat is thick or considerably reduced. The endosperm is reduced, usually not discernible except in the Spiraeae; nucellus is apparently absent. The mature seed is almost en-

tirely filled by the straight, plump, dorsally convex cotyledons. The radicle is short, straight, directed toward the hilum.

EXTERNAL CHARACTERISTICS

There is scarcely any one shape or form that can be said to be characteristic of the seeds or seed-like structures of the Rosaceae; widely divergent aspects are assumed by different members of the family. Those of the Spiraea tribe are generally elongate, tapering at both ends; the achenes of the Potentilla tribe are commonly compressed but may be elongate and beaked *(Geum);* achenes of *Rosa,* the sole member of its tribe, are slightly elongate, blocky-angular, or somewhat sectoroid; seeds of the apple tribe are also usually elongate, commonly biconvex to sector-shaped in cross section; the seeds (stones) of the Prunus tribe are spheroid to ellipsoidal in general form.

In those genera where we have to deal with true seeds, the hilum is commonly quite distinct; it is usually subterminal in position, at, or near the end of, a longitudinal ridge or suture (the raphe). Achene forms frequently exhibit two scars or hilum-like structures. One of these is the true attachment scar; the other represents the point of attachment of the deciduous style.

Considerable variation is, likewise, exhibited by surface configuration. The true seeds are most commonly nearly smooth, sometimes appearing polished. Achene-bearing species possess seed-like structures which are smooth or variously roughened. Stones of the Pruneae may be smooth, irregularly corrugated, or alveolate.

ASSOCIATED STRUCTURES

The divergence in number, position relative to other floral parts, and mode of development of the carpels in the Rosaceae is reflected in a corresponding variation in structures associated with the seeds. The nature of these various accessory structures has, in part, been discussed above.

The pistils range from one to many. They may be borne in an apical concavity of the depressed apex of the floral axis (hypanthium); they may be attached to a central column arising from the center of the hypanthium, or they may be completely enclosed by the hypanthium.

In the Spiraeae, Potentilleae and Rubeae the pistils (each single carpels) are numerous, free from each other and the hypanthium. In the Spiraeae they are several-seeded and ripen as follicles from which the true seeds separate at maturity. In the other two tribes, the pistils are one-seeded, in the Potentilleae ripening as achenes, in the Rubeae maturing as an aggregate of small fleshy "drupelets." In the Poterieae and Roseae the pistils, one to many, are enclosed within the membranous,

bristly or fleshy hypanthium. Each is one-seeded and matures as an achene. In the Rosaceae these commonly eventually separate from the so-called fruit (the "hip"), but are more or less permanently enclosed in the Poterieae. The pistil is solitary (compound or simple) in the Pomeae and Pruneae, ripening into a fleshy fruit or spurious fruit (Pomeae). The seeds (true seeds) are several in the Pomeae and are contained within the carpel-cells which are in turn surrounded by an enclosing succulent, hypanthial or appendicular structure. The single seed of the Pruneae is enclosed within a stony endocarp; thus this "seed" or stone is a seed plus the inner layers of the pericarp covering.

CLASSIFICATION BY SEED CHARACTERS

As might be inferred from the above context, a classification of the Rosaceae on the basis of seed characters *per se* would scarcely seem to be practical. The major groups of this family can, however, frequently be delimited on the basis of differences in the accessory structures surrounding and associated with the seeds; these differences are briefly discussed in the preceding section.

LEGUMINOSAE

(Plates 5, 6)

GENERAL CHARACTERISTICS

Seeds extremely various in form, most commonly laterally elongate or compressed-ovoid, frequently with a marginal notch or lobe, sometimes irregularly obovoid from a pointed base. Hilum contiguous to the lobe or notch, rarely (in our species) basal; in appearance, circular to oblong, frequently quite conspicuous and ornamented by various surrounding markings. Seed coat smooth, rarely papillose, frequently very thick and hard. Cotyledons straight, usually ovate or elliptic in outline. Radicle usually curved along margin of cotyledons (straight in some forms) short or long. Plumule frequently well developed. Endosperm present or appearing absent.

MORPHOLOGY

The seeds develop from anatropous (Mimosoideae and Caesalpinoideae) or campylotropous (Papilionoideae) ovules.

The seed coat[4] is usually well developed and comprises a thick and hardened protective covering. It is, in many genera, quite impervious to water until broken or injured; so-called "hard seeds" of such legumes may lie in the soil for several years be-

[4]The nature of the seed coat has been intensively studied by numerous workers, both by those interested strictly in the anatomical nature of this structure and by investigators dealing with the underlying causes of delayed germination. Extensive reference lists are given by Pammel (25) and Netolitsky (24).

fore germination. Accompanying the considerable development of the seed coat is a corresponding specialization of the component layers. The outermost row of cells, strongly elongated radially, is generally known as the palisade, or malpighian layer. The so-called light-line usually transverses the upper extremity of these cells. The second cell tier, characteristic of many but not all legumes, is most frequently termed the osteosclerid layer. The component cells are flattened and frequently medially constricted. Internal to the osteosclerids, a parenchymatous region is generally present; it is several tiers of cells in thickness. In a few genera the seed coat is greatly reduced, the pericarp of the fruit having taken over the protective function; *Arachis* and *Stylosanthes* may be mentioned as examples.

Contrary to many statements made about the Leguminosae, endosperm is usually present and frequently in considerable amount. In many representatives of the Mimosa and Senna subfamilies the endosperm-contained stored food is equal or greater in bulk than that contained in the cotyledons. Endosperm is likewise evident upon gross inspection in the Papilionoideae in the tribes Podalyrieae, Psoraleae, Genisteae, Galegeae and some of the Trifoleae and Hedysareae; it is not evident in the Phaseoleae or Vicieae but according to Pammel (25) is usually present in small amounts.

The embryo, lying internal to the endosperm, consists of two large, straight cotyledons, a short or somewhat elongated radicle, a rudimentary or well-developed plumule. The cotyledons are entire, circular to oblong in outline, most commonly elliptic-ovate. The radicle is various; in most of our species it is curved about the margin of the cotyledons (sometimes continuing nearly the entire length of the seed) or divergently directed relative to the long axis of the seeds; in the Mimosoideae and Caesalpinoideae, however, it is short, straight and strictly basal.

EXTERNAL CHARACTERISTICS

Leguminous seeds are, perhaps, most characteristically subreniform or ovoid in shape, with or without a marginal notch. A multitude of other forms may, however, be found throughout the family. These range from spheroid, as are the seeds of many of the Vicieae, to oblong, angular or compressed forms characteristic of other groups; the seeds of many of the Mimosoideae are flattened and strongly pointed toward one end.

The frequent presence of a marginal notch or lobe is due to the failure of the tip of the curved radicle to terminate flush with the cotyledons; the position of this lobe is determined by the length of the radicle relative to the cotyledons. In some seeds a distinct furrow or line between the radicle and the cotyledons is also evident externally.

The hilum is marginally placed, located just beyond the termination of the radicle and in the marginal notch, if the latter is present. It is quite varied in different members of the family, is often large and correspondingly striking in appearance. In shape, it ranges from circular to narrowly oblong. It may be flush with the surface or sunken, is sometimes carunculate, frequently possesses a narrow longitudinal slit, and may be variously surrounded by protuberances, ridges, lines or furrows. This surrounding area is also often differently pigmented than the rest of the seed. The micropyle is located in proximity to the hilum but is frequently not superficially discernible.

In most legumes the seed coat is smooth or nearly so. In a few groups, particularly the Podalyrieae and Vicieae, it may be irregularly roughened or warty.

ASSOCIATED STRUCTURES

The typical fruit of this family is a pod or legume. This is a one to several-seeded unicarpellate structure, ordinarily dehiscent along two sutures but at times indehiscent. In many representatives of the tribes Hedysareae and Psoraleae the pod is not only indehiscent but is closely persistent about the seeds so that the latter are not observable unless artificially removed. The pods are variously shaped, usually somewhat laterally compressed, commonly reticulate or hairy, are glandular in the Psoraleae.

CLASSIFICATION BY SEED CHARACTERS

Brief descriptions of principal seed characteristics of the subfamilies and some of the important tribes of this family are given below. There are sharp morphological distinctions between the Papilionoideae and the other two subfamilies, and the seed of these two groups can usually be easily distinguished. The descriptions of the tribes within the Papilionoideae should be regarded as representing tendencies only; due to the presence of many exceptional forms, sharp lines of divergence cannot be drawn. It might be indicated, however, that many genera and species within these tribes possess very distinctive seed characters (principally relative to shape, the nature of the hilum and its surrounding ornamentation) by means of which they can be readily identified.

1. SUBFAMILIES CAESALPINOIDEAE AND MIMOSOIDEAE

(The plants belonging to these groups are mostly tropical or native of other lands and are poorly represented in our flora.)

Seeds longitudinally elongate, ellipsoidal, obovoid or irregularly shaped, compressed or plump, generally rounded at apex and tapering at base. Surface smooth or roughened, each of the faces frequently with a conspicuous elliptical line which is open

at basal end. Hilum basal or obliquely sub-basal at the narrow end, usually small and inconspicuous but with various surrounding ornamentation. Radicle short, straight. Cotyledons usually rather thin. Endosperm abundant, commonly containing the greater portion of the food reserves.

2. SUBFAMILY PAPILIONOIDEAE

Seeds various in shape, not tapering to a narrow base. Hilum frequently conspicuous, usually appearing apical or lateral; if terminal at the broad end of the seed, commonly in a marginal notch or approached by a conspicuous radicular lobe. Radicle curved, often large and well developed. Endosperm evident in all tribes except Vicieae and Phaseoleae but main portion of food reserves in cotyledons.

Galegeae (Characteristic genera: *Astralagus, Oxytropis, Sesbania.)* Seeds laterally elongate or about as high as wide. Hilar margin lobed, notched or entire. Hilum circular or elliptic, sometimes carunculate. Endosperm usually evident, often copious.

Genisteae (Characteristic genera: *Lupinus, Crotalaria, Cytisus.)* Seeds sidewise compressed to plump-ellipsoidal. Hilum basal (or frequently oblique in *Lupinus),* usually in a notch or concavity; in appearance large, elliptical, generally sunken, sometimes carunculate. Endosperm evident.

Hedysareae (Characteristic genera: *Desmodium, Lespedeza, Hedysarum.)* Seeds mostly ovoid or laterally elongate, commonly notched on hilar margin. Hilum generally lateral, small, circular, scarcely ornamented. Endosperm very thin or not discernible. Seeds frequently persistent within the closely adherent pods or pod-segments.

Phaseoleae (Characteristic genera: *Phaseolus, Vigna, Strophostyles.)* Seeds oblong, elongate-reniform to subspherical, laterally compressed or plump, "blocky" or "chunky." Hilum lateral to sub-basal, usually conspicuous, circular to oblong, variously ornamented, not uncommonly carunculate. Radicle short; plumule usually well developed; endosperm not evident.

Podalyrieae (Characteristic genera: *Baptisia, Thermopsis.)* Seeds ovoid or laterally elongate. Hilar margin notched, emarginate, or the radicle forming a marked protuberance. Hilum lateral, usually basally offset, circular, small and not particularly ornamented. Seed coat frequently roughened in *Baptisia.* Endosperm plentiful.

Psoraleae (Characteristic genera: *Amorpha, Glycyrrhiza, Psoralea.)* Seeds laterally elongate to subcordate. Notch apical or lateral, inconspicuous, or with a strongly out-turned radicle lobe. Hilum laterally offset or less frequently subterminal, circular, variously ornamented. Endosperm evident but not strongly developed. Seeds commonly retained within the indehiscent, glandular or sometimes spiny *(Glycyrrhiza)* pods.

Trifoleae (Characteristic genera: *Trifolium, Melilotus, Medicago.)* Seeds mostly compressed-ovoid, laterally elongate or higher than wide, terminally or laterally emarginate. Hilum subterminal to lateral, small and unornamented. Endosperm evident but not copious. Radicle well developed, frequently nearly as long as cotyledons.

Vicieae (Characteristic genera: *Vicia, Pisum, Lathyrus.)* Seeds irregularly spherical to lenticular, smooth or irregularly roughened. Hilum sub-basal, flush, usually oblong or narrowly oblong with a conspicuous medial slit, variously otherwise ornamented. Cotyledons massive; radicle short; plumule usually well developed. Endosperm much reduced.

EUPHORBIACEAE

(Plate 6)

GENERAL CHARACTERISTICS

Seeds ovoid to biconvex or plano-convex, sometimes subspherical, sectoroid or quadrangular. Hilum subterminal at narrow end, commonly carunculate. Seeds possessing a distinct longitudinal suture (raphe) extending from hilum to opposing (chalazal) end. Seed coat smooth or variously rugose, channeled or scurfy.

Endosperm present, abundant. Embryo usually straight, medial and longitudinally directed. Cotyledons thin and broad; radicle short or long.

Seeds apically pendent, one, or less commonly two, in each locule of the three-chambered capsule.

MORPHOLOGY

The ovules are usually anatropous possessing two integuments. The seed coat is strongly developed, often thick and stony, usually with several distinct regions including a well-marked palisade layer. The nucellus is absent or rudimentary. The endosperm is abundant, filling the greater portion of the seed cavity. The embryo is longitudinally directed, medially placed, straight or sometimes curved (Phyllanthoideae), approaching the length of the seed or considerably shorter. In all of our species the cotyledons are thin, frequently evidently nerved, flat, elliptic to oblong in outline, abruptly broader than the hypocotyl or radicle. Their position is such as to be parallel with the dorsoventral aspects of the seed.

EXTERNAL CHARACTERISTICS

The most distinctive external morphological characteristic of this family is the raphe or ventral suture. This structure is evident as a longitudinal darkened line or seam which is medially

placed on the "ventral" side of the seed and extends from the hilum to the chalazal area at the opposite end.

In general form, the seeds are most commonly ovoid or compressed-ellipsoidal or plano-convex, occasionally varying to quadrangular (some species of *Euphorbia)* or spherical *(Tragia);* those of the tribe Phyllanthoideae, borne two in each cell of the capsule, are frequently sectoroid. The ventral face is frequently nearly plane while the opposing dorsal surface is distinctly convex; the resulting plano-convex form is particularly characteristic of the genus *Croton.* In other cases the ventral aspect may be curved or even distinctly angled. Such an angle, if present, is at the suture, thus dividing the face into two distinct aspects. This is the case in those species of *Euphorbia* possessing quadrangular seeds and in members of the genus *Phyllanthus* where the two ventral aspects appear as converging lateral sides.

The hilar area is obliquely subterminal on the ventral aspect. While the hilum proper may be rather small, the surrounding specialized area is frequently rather large and somewhat sunken. It is commonly partially obscured by the caruncle, a laterally drawn out, irregularly ring-like callus outgrowth. This structure is characteristic of many of the Euphorbiaceae but is not invariably present.

The chalazal area, opposed to the hilum, is marked principally by a dark-pigmented enlargement of the suture.

Surface ornamentation is various. In many species the seed is almost entirely smooth, sometimes blotched or scurfy. In the genus *Croton* it possesses a glossy, marbled texture. Typical markings include striations, reticulations, alveolae, irregular furrows or laterally extended sunken areas.

ASSOCIATED STRUCTURES

The fruit of most of the North American members of this family is a three-lobed, frequently oblate-compressed, subspherical capsule. It is usually hard and leathery or coriaceous in texture, commonly warty or hairy. Internally the fruit is triloculate, one locule corresponding to each lobe. Each locule cavity in most of our species bears a single seed; *Phyllanthus* and related genera possess two seeds to each locule.

The seeds are longitudinally placed in the capsule and are attached apically to the central column, i. e., the hilum end uppermost. They (the seeds) are laterally oriented so that the ventral suture lies against this column; thus their dorsal aspect is contiguous to the outer wall of the capsule while the ventral surface follows the contours of the partitions on either side. In the case of *Phyllanthus* the position of the seeds is similar to that of other genera except that two of them lie side by side; this juxtaposition is obviously responsible for their typical sectoroid shape.

The capsules are dehiscent but frequently tardily so, so that the seeds are contained after maturity.

CLASSIFICATION BY SEED CHARACTERS

The two subfamilies represented in the North American flora, the *Crotonoideae* and the *Phyllanthoideae,* may be distinguished by the shape of the seeds and the number in each capsule. These distinctions have previously been discussed. The former group contains most of our species.

Seed characters are more or less distinctive for many genera and species and may allow reliable identification. Murley (14) has prepared a treatment of the Euphorbiaceae in Iowa based primarily upon seed characters; species concerned are illustrated. Wheeler's (38) taxonomic treatment of the subgenus *Chamaesyce* of *Euphorbia* includes detailed descriptions of seeds and capsules, likewise illustrations.

MALVACEAE

(Plate 7)

GENERAL CHARACTERISTICS

Seeds sectoroid to compressed or subspherical; in face view circular to irregularly ovate. Margin commonly strongly notched. Hilum flush or depressed within the notch, with a characteristic grill-like appearance, initially obscured by a flattened caruncle-like structure. Seed coat usually strongly developed; surface nearly smooth to rough or warty, sometimes hairy.

Endosperm present, sparse or abundant. Embryo large, curved, the cotyledons much convoluted.

Seeds commonly persistent within carpel wall; this seed-like carpel sectoroid, membranous or indurate, frequently reticulate or hairy, sometimes spiny-pointed.

MORPHOLOGY

The ovules are usually campylotropous but are anatropous in *Gossypium* and related genera. The integuments are two in number, commonly rather thick.

The seed coat is characteristically thick and durable, commonly impervious to water. Of its several layers, the following are distinctive: a thin external or outer pigment layer (derived from outer integument), a strongly lignified palisade layer and an inner pigment row (latter two derived from inner integument). In most cases at least some of the epidermal cells give rise to external elongations or hairs, but these are frequently not persistent on the mature seeds.

The nucellus is absent or composed of a single layer of cells.

Endosperm is present, scanty or abundant depending upon the nature and size of the embryo.

The cotyledons are very large, commonly subcordate or basally lobed, frequently nerved, sometimes finely hairy or glandular. They lie against one another and are rolled or convoluted in various fashions, usually being doubled up or turned in, both longitudinally and laterally. Thin layers of endosperm are frequently present between the cotyledons.

The morphology of various malvaceous seeds is discussed by Reeves (29, 30); *Gossypium* is treated in detail by Simpson, Adams and Stone (34).

EXTERNAL CHARACTERISTICS

The seeds of the Malvaceae tend to fall into two groups or types dependent upon the nature of the fruit in which they originate. In the Hibisceae, borne in a loculicidal capsule, they are plump-compressed to ellipsoidal or subspherical. In the Ureneae and Malveae the fruit is a schizocarp which splits radially into separate carpels. The seeds, mostly one to two in each carpel segment, are usually laterally compressed in a sectoroid fashion. Their lateral faces are, in general, subcircular or obovate, commonly narrowed, short truncate, and asymmetrically lobed or notched at the ventral margin.

The hilum is depressed within the above-mentioned ventral notch or, in the Hibisceae, flush with the surface. It is usually initially obscured by a flattened, somewhat caruncle-like structure (funiculus remnants?) which extends up and is adnate to the radicular lobe. The hilum is commonly very characteristic. It possesses a short longitudinal hilar slit surrounded by blackish radiating lines which give it a distinctive grill-like appearance.

The seed surface is hard, nearly smooth or somewhat scurfy. Under low magnification it is usually seen to be cellular-pitted or papillose. It may be warty-papillate as in *Hibiscus trionum,* in many genera is sparsely hairy, especially in the neighborhood of the hilum—very densely hairy in *Gossypium.*

ASSOCIATED STRUCTURES

The pistil of the Malvaceae is a several-carpellate structure, at maturity forming a loculicidal capsule or a schizocarp. In the latter case, the pericarp of the individual separating carpels is commonly indehiscent and remains as a persistent covering about the usually solitary seed (carpels somewhat dehiscent in *Abutilon* and *Sphaeralcea,* seeds two to several). These seed-like carpel units are sectoroid in shape, externally membranous or hard, frequently hairy, sometimes pointed or spine-tipped. The faces are commonly possessed of low radial ridges or concentric lines and are distinctly marginally delimited. The ventral edge, frequently notched, coincides with that of the seeds.

CLASSIFICATION BY SEED CHARACTERS

The seeds of most of the members of Malvaceae observed are quite distinctive and allow identification, at least to genus. The seed characters used in conjunction with those of the associated carpels make feasible an approximate definition of the principal divisions of the family. Representatives of all three of the major tribes may be found in this country, although the greater number of our common plants are included in the Malveae. A tabulation of these groups is presented below:

1. Fruit a schizocarp, the individual carpels and seeds sectoroid in shape.
   2. Carpels usually more than five in number, seeds and carpels thus mostly compressed-sectoroid (i. e., dorsal margin thin); ventral margin (of both seeds and carpels) short, usually notched; dorsal margin strongly curved (more than 180°); seeds about as wide as long or elongate at right angles to ventral margin.
      Tribe: *Malveae.*
      3. Seeds several in each carpel, which is usually dehiscent at maturity.
         Subtribe: *Abutilinae* (e. g., *Abutilon, Modiola).*
      3. Seeds one in each carpel, the latter commonly indehiscent and retaining the seeds.
         Subtribes: *Malvinae* and *Sideae* (e. g., *Malva, Althaea, Sida, Callirhoë).*
   2. Carpels five in number, seeds thus sectoroid with a broad dorsal margin; ventral margin (of both seeds and carpels) elongate, usually not notched; dorsal margin not strongly curved (less than 180°); seeds somewhat elongate parallel to ventral margin.
      Tribe: *Urenеae* (e. g., *Urena, Pavonia).*
1. Fruit a capsule, seeds not sectoroid in form.
   Hibisceae (e. g., *Hibiscus, Kosteletzkya, Gossypium).*

UMBELLIFERAE

(Plate 7)

GENERAL CHARACTERISTICS

Seeds (one-seeded fruits) longitudinally elongate, short and plump to narrowly oblong, plano-convex to polygonal or strongly flattened, borne in longitudinally united pairs. Surface commonly lengthwise ribbed or nerved, ribs frequently five in number. An apical, conical or depressed structure (the stylopodium) is frequently present.

Pericarp tissue usually corky, commonly rather thick, inde-

hiscent but separable from seed within. Endosperm abundant. Embryo very small, apical; radicle directed upwards and cotyledons down.

MORPHOLOGY

The ovary of the Umbelliferae is an inferior, two-celled structure. The ovules are two in number, one in each cell, are anatropous, possessed of a single integument, and are suspended from the apex of the cell. At maturity the ovary splits longitudinally (i. e., the cells separate) into two one-seeded portions. This fruit is commonly known as a schizocarp ("splitting fruit") and the component segments as mericarps. The mericarps are the seed-like disseminating units of this family, hence are the structures popularly designated as seeds.

The true seed is completely surrounded by the indehiscent pericarp but is not adherent to this tissue. It possesses a thin, unornamented seed coat, usually of a single layer of cells; the seed coat is cutinized both within and without. The nucellus is absent in mature seeds, and the abundant endosperm fills nearly the entire cavity. The embryo is small, consisting of a short, straight radicle and small, closely-appressed cotyledons—in some cases only one cotyledon appears to be present. The apical and inverted position of the embryo in the mericarp is due to the pendent (thus upside down) position of the seed; the embryo is really basal (i. e., as regards the true seed) with a downwardly directed radicle.

The pericarp tissue may be thin or thick and is frequently differentiated into several layers. Superficial corky thickenings are commonly present and appear externally as longitudinal ribs. Conspicuous oil ducts are characteristic of many members of this family. These run parallel to the ribs and are usually located in the interspaces between them; they are quite variable as to number, size and nature of aromatic contents. Vascular bundles and mechanical tissue can commonly be observed, particularly in the ribs.

EXTERNAL CHARACTERISTICS

The seeds are elongate (sometimes nearly equidimensional) along an axis parallel to the plane of fission from one another. They are flat or somewhat longitudinally concave on the ventral, joining (commissural) face; are variously convex, angled or nearly flat on the opposing surface or surfaces. They are asymmetrical in cross section and in the plane parallel to the commissural side, but may be divided nearly symmetrically by a longitudinal section at right angles to commissure. The seeds are generally widest near the base and taper toward apex, thus are semi-ovoid or semi-conic[5]; strongly elongate forms such as

[5]The entire schizocarp is conic or ovoid, and each mericarp represents a longitudinally divided half.

Osmorrhiza or *Cryptotaenia* may taper toward both ends. In genera such as *Pastinaca* and *Heracleum* the seed is strongly compressed dorsally, thus exhibiting broad, flat commissural and dorsal surfaces with the lateral portion reduced to an edge. Cross sectionally the seeds vary from semi-circular or wedge-shaped to angular and several sided; in compressed forms they may be very narrowly rectangular. The commissure is quite broad in flattened seeds such as those of *Pastinaca* but may be extremely narrow as in *Bifora* or *Petroselinum.* In some genera (i. e., *Conium, Chaerophyllum)* the commissure possesses a conspicuous medial longitudinal furrow.

The seeds of the greater number of the members of this family are longitudinally ribbed. The usual number of these structures is five: a centrally-placed dorsal rib and two paired lateral ones on each side; commonly the outside laterals delimit the margin of the commissure, and the other pair are medially located between them and the dorsal rib, but various displacements may be present. As to structure the ribs may be very strong, thick and corky; they may be obscure, representing merely the angles of the mericarp; they may be thin nerve-like ridges or may be drawn out into wing-like extensions. Seeds of some species possess ribs of more than one type; for instance in *Pastinaca* or *Prionosciadium* the marginal ribs are greatly enlarged, the others, conversely, are nerve-like and non-distinctive. Additional ribs are occasionally present. These, the so-called secondary ribs, consist of two pairs and alternate with primary ones as in *Daucus.*

Surface markings other than, or in addition to, ribs may occasionally be present. These are barbs in the genera *Torilis* and *Osmorrhiza;* barbs or prickles localized on the secondary ribs, *Daucus;* warts or scales, *Eryngium.* The oil tubes lying in the intervals between the ribs are frequently visible externally as dark lines.

The stylopodium consists of the remnants of the persistent style. It is conical to skull-cap-like in shape and occupies an apical position on the schizocarp; it is of similar face outline on the seeds but divided lengthwise. It may be flattened with flange-like edges or considerably higher than wide. In some genera it is obsolete.

ASSOCIATED STRUCTURES

The remnants of the calyx sometimes persist as five small lobes on the apex of the schizocarp.

CLASSIFICATION BY SEED CHARACTERS

The nature of the seeds or mericarps is most important as a basis of classification within this family. Most of the genera have been defined with reference to the structural characteristics of the mericarps, and can be recognized by such characters.

CONVOLVULACEAE

(Plate 8)

GENERAL CHARACTERISTICS

Seeds irregularly sectoroid or "lumpy-rounded," commonly somewhat broader at one end than other. Hilum subterminal at narrower end, rounded or elliptic in outline, usually large, frequently conspicuous. Seed coat granular-roughened or scurfy, sometimes tuberculate, papillose or hairy.

Endosperm present. Embryo with a straight radicle-hypocotyl portion, and much folded or convoluted cotyledons; that of *Cuscuta* is spirally coiled and without cotyledons.

Fruit a two to four-celled capsule with one to two seeds in each chamber.

MORPHOLOGY

The ovules are more or less anatropous and possess a single integument.

The seed coat is generally thick and strongly developed. It usually possesses one to two palisade layers, outside and inside of which are smaller cubical, sometimes somewhat crushed cells. In some forms it is strongly infolded in the neighborhood of the hilum, forming a short, internal septum.

No nucellus is present in mature seeds. The endosperm is present in all forms but is frequently in various stages of disintegration and not strongly evident.

The embryo, except in *Cuscuta,* typically possesses a short, straight radicle-hypocotyl portion and very broad, thin, convoluted, frequently lobed (both apically and basally) cotyledons. The folding of the cotyledons varies in different forms; these structures are perhaps most typically doubled longitudinally and laterally rolled about the radicle. The embryo as a whole, however, appears nearly straight; the cotyledons, although contorted as above indicated, are nearly continuous with the axis of the radicle and exhibit no continued longitudinal curve. This is in contradistinction to the Malvaceae which also possess convoluted cotyledons but in which the embryo as a whole is curved.

The parasitic genus *Cuscuta* is an exception to all other forms. The seeds of these plants possess spirally coiled embryos without cotyledons.

EXTERNAL CHARACTERISTICS

The outline of the seeds of this family varies from a somewhat angular subspherical form to an elongate, three-angled or sectoroid shape. The elongate forms are generally conspicuously thicker and wider at one end than the other; the convex dorsal

surface curves up to this end in a somewhat dome-shaped fashion. The two ventral faces are mostly sub-equal, plane or slightly convex.

The hilum is sub-basal at the narrow extremity, usually obliquely placed on the ventral angle; this orientation is scarcely evident in rounded seeds of *Cuscuta.* It is generally large and conspicuous, subcircular or elliptic, flush or sunken.

The seed coat surface is most commonly irregularly roughened or minutely tuberculate; in the genus *Cuscuta* it is frequently conspicuously scurfy in appearance.

ASSOCIATED STRUCTURES

The ovary of the Convolvulaceae is usually two or sometimes three-carpellate. The fruit is a capsule with as many locules as carpels, or twice as many due to the intrusion of secondary partitions. The seeds are most commonly four to six in number, i. e., two in each cell, or they may be reduced to one or two. They are axially attached near the base of the ovary. This position, when a full complement of seeds is present, tends to result in the irregularly sectoroid shape characteristic of many species; when the number is reduced (as in many species of *Cuscuta)* a subspheroid shape results.

In most of our forms the seeds readily separate from the capsules at maturity.

CLASSIFICATION BY SEED CHARACTERS

Little can be indicated relative to the potentialities of classification of members of this family by seed characters. Musil (21) describes seeds of various species of dodder occurring with crop seeds.

LABIATAE

(Plate 8)

GENERAL CHARACTERISTICS

Seeds longitudinally elongate, with one convex dorsal side and two plane ventral faces, or nearly rounded in cross-section. Basal end of seed (i. e., where scar is located) usually narrowed or pointed; apex rounded. Scar ventral-basal, usually small and non-distinctive, occasionally large, sometimes ornamented by white spots or lines. Seed surface usually smooth, reticulate or papillose in a few genera.

Embryo filling most or all of seed cavity. Cotyledons large, flattened parallel to dorsal and ventral aspects, straight. Radicle short, often only slightly exerted beyond cotyledons, basally directed, straight or rarely curved.

MORPHOLOGY

The ovules are basal, usually anatropous. Integument one. The labiate seed is not a true seed but a one-seeded segment of the fruit. Botanically, it is termed a nutlet. It develops from a four-lobed ovary, each lobe of which is unilocular and contains a single ovule. These separate at maturity, the resultant individual units each consisting of a seed surrounded by a hardened indehiscent pericarp shell. In a few genera, one or several of these units abort and are not seed-bearing.

The seed coat in the mature seed is usually considerably reduced and frequently consists of only a thin membrane. The pericarp, on the other hand, is often considerably thickened and well supplied with mechanical tissue.

Endosperm is, for the most part, poorly developed. Genera in which a distinct endosperm layer was observed include *Stachys, Perilla, Physostegia, Moluccella* and *Scutellaria.*

The embryo is straight (except in *Scutellaria)* with large cotyledons and a short radicle and hypocotyl. The cotyledons are flattened in the dorso-ventral plane, lie appressed to one another, and are shaped to fit the longitudinal contours of the seed. The radicle is short-protuberant below the cotyledons or is sometimes scarcely exserted and lies almost entirely between them. The cotyledons are frequently attached to the hypocotyl somewhat above their basal extremities, in which case they are usually lobed or provided with a narrow notch extending up to the point of attachment.

Scutellaria is the principal divergent form as regards embryo morphology. In this genus the embryo is obliquely placed in the seed; the radicle is much longer than in other genera, is recurved, and lies appressed to the back of one of the cotyledons.

EXTERNAL CHARACTERISTICS

The shape of the nutlets is fundamentally sectoroid. The flat (or slightly convex) ventral sides meet at right angles or nearly so. The angle of these surfaces with the curved dorsal aspect likewise approximates 90 degrees. This configuration, conditioned by the origin of the nutlets as segments of the ovary, is, with certain modifications, peculiar to the Boraginaceae and Verbenaceae as well as this family.

In those genera in which some of the nutlets abort, the form of those nutlets which develop is correspondingly modified from the typical appearance above described. The seeds of other members of the family may likewise be somewhat at variance with the typical form aside from any failure of maturation of certain portions of the pistil. In some genera the marginal angles are rounded off and the delimitation of the surfaces correspondingly obscured. The reduction of the ventral angle, the ventral side

thus presenting a continuous convex surface, is much more common than the elimination of the dorso-ventral angle, but the latter condition is to be found in such genera as *Hedeoma* and *Thymus*. The apical portion of the seed, representing the free lobe of the ovary, is usually rounded and not strongly angled.

In face view the nutlets mostly present an obovate or oblong appearance; they are generally both wider and thicker at apex than at base. The apex is usually rounded but is sometimes sharply truncate *(Leonurus)*; the base generally pointed or narrowly truncate.

Scutellaria is at variance with most of the other members of the family as regards external form. The seeds are irregularly plump-compressed with two suborbicular or obovate, convex faces. On one face a distinct rounded ridge (the radicle) is evident extending about halfway up the seed. Seeds of the genus *Lycopus* possess a broad marginal wing.

The scar area is basal or sub-basal on the ventral side, frequently oblique. It may be flush with the surface or in a shallow notch; the ventral angle may or may not continue through it. It is usually small and inconspicuous but, contrariwise, may be large and so ornamented as to present the most striking features of the seed. Such ornamentations most frequently consist of callus-like white spots or lines; these are exemplified by certain species in the genera *Nepeta, Dracocephalum* and *Lavandula*. A distinctive white, pointed caruncle is present in *Prunella vulgaris*. In *Teucrium* and *Ajuga* the scar is very large and frequently exceeds one-half the height of the seed.

The seed surface is characteristically smooth; cellular reticulations or roughening can be observed only under fairly high magnification. Deviations include the genera *Teucrium* and *Ajuga,* which are coarsely and conspicuously reticulate, and *Scutellaria,* which is bumpy-papillose. *Prunella* is quite shiny in contrast to the relatively dull appearance presented by other members of the family; when soaked in water these seeds become very mucilaginous. Epidermal hairs, usually at the apex of the nutlet, are evident in a few genera, i. e., *Agastache* and *Leonurus.*

ASSOCIATED STRUCTURES

Except possibly for calyx fragments, accessory structures are rarely found associated with the nutlets. The labiate calyx is tubular, three to five-toothed, sometimes two-lipped, frequently with strong longitudinal nerves.

CLASSIFICATION BY SEED CHARACTERS

Three tribes of this family represented in this country may be differentiated as follows:

(1) *Ajugeae*—Scar area very large, extending about halfway

up ventral side of seed. Surface coarsely reticulate. Radicle straight.

(2) *Scutellarieae*—Scar small. Seed surface papillose-roughened. Radicle recurved and upwardly directed.

(3) *Stachyeae*—Hilum area various, not approaching one-half length of seed. Surface smooth. Radicle straight.

Most of the North American representatives of this family are in the latter tribe. It seems possible to recognize most species by seed characters, but whether the genera are consistent enough to render a classification by such characters feasible it is not currently possible to say.

SOLANACEAE

(Plate 9)

GENERAL CHARACTERISTICS

Seeds mostly compressed, thin or thick, subcircular to elliptic in outline, sometimes nearly equidimensional or slightly elongate. Hilum marginal or (in elongate forms) subterminal. Surface usually cellular, reticulate, alveolate or papillate, sometimes appearing glandular, rarely nearly smooth.

Endosperm present, usually abundant. Embryo with narrow cotyledons, strongly curved or, in a few forms, nearly straight.

Fruit a capsule or a berry.

MORPHOLOGY

The ovules are anatropous to campylotropous and possess a single integument. The mature seed coat consists of mostly two to four layers of parenchymatous or crushed cells; palisade tissue is not present. The component cells are commonly wavy or sinuate margined. Sometimes the epidermal layer is partially broken down so that only the lateral walls of the cells are persistent, the seed coat thus appearing like an empty meshwork. In other cases, the cells of this outer layer are further reduced, ultimately consisting only of radially extended thickened portions of the side walls which, in the mature seeds, simulate hairs (e. g., *Lycopersicon*). Endosperm is present in all of our representatives of the family and is usually abundant. The embryo is strongly curved in most species, extending through an arc approaching or exceeding 360°. The cotyledon tip terminates near the base of the radicle or is somewhat spirally incurved. The edges of the cotyledons are toward the flat side of the seed. In the Cestreae and Salpiglossideae, on the other hand, the embryo is straight or nearly so, tubular with narrow, thick, appressed, laterally straight (dorsally convex) cotyledons.

EXTERNAL CHARACTERISTICS

The seeds of most of our representatives of the Solanaceae (tribes Solaneae, Datureae and Nicandreae) are distinctly flattened, thick or thin, irregularly rounded to elliptic or lopsided in outline. Those of the Cestreae and Salpiglossideae are usually much smaller than in the above-mentioned groups and are irregularly cubical to slightly elongate and rounded-quadrangular. The hilum is marginal in the majority of our forms (the compressed-seed group), sometimes in a submedial notch, sometimes offset or occupying a symmetrical corner projection. It may be either nearly flush or depressed in a short, sometimes conspicuous, marginal groove. In species observed of the Cestreae-Salpiglossideae group the hilum is subterminal and flush with the surface or nearly so.

The seed surface is usually finely reticulate, deeply mesh-like or punctate, sometimes appearing striate with minute depressions arranged in lines.

ASSOCIATED STRUCTURES

The fruit of the Solanaceae develops from a two-carpellate, usually two-celled superior gynoecium. At maturity it may be dry (a capsule) or fleshy (a berry). The ovules and seeds are numerous and are borne on axillary placenta. Seeds separated from fleshy-fruited members of this family are often partially obscured by adherent dried fruit fragments.

CLASSIFICATION BY SEED CHARACTERS

As previously indicated, two quite different seed types are to be found in this family. The flattened form with a strongly curved embryo is characteristic of the Nicandreae, Solaneae and Datureae; the small cubical or elongate type with a straight embryo is generally found in the Cestreae and Salpiglossideae.

PLANTAGINACEAE[6]
(Plate 9)

GENERAL CHARACTERISTICS

Seeds elongate, boat-shaped to irregularly angular-compressed or "lumpy." Hilum medial, depressed in ventral concavity in some forms. Surface smooth, minutely punctate, striate or sometimes rugose.

Embryo longitudinally placed, straight, with relatively narrow, flatwise disposed cotyledons. Endosperm scanty or plentiful, usually completely surrounding embryo.

Fruit a circumscissile capsule bearing two to many seeds.

MORPHOLOGY

The ovules are more or less anatropous; each bears a single, thick integument.

[6]This discussion pertains specifically to the genus *Plantago*.

The seed coat is well developed, usually of several layers. Upon exposure to moisture it characteristically breaks down into a slimy mucilaginous material.

The endosperm is present, scanty or thick, commonly completely embedding the embryo. The embryo is straight, longitudinally directed and approaches the length of the seed. It is of nearly the same width for most of its length and tapers evenly at the base with no sharp demarcation between cotyledonary and radicle-hypocotyl portion. The position of the embryo relative to the axis of the seed and the thickness of the cotyledons varies in different forms. In species such as *Plantago lanceolata* and *P. aristata* (seeds strongly boat-shaped) the cotyledons are as thick as, or thicker than, wide, and in face view are oriented at right angles to the dorso-ventral surfaces of the seed. In forms such as *P. rugellii* and *P. major,* the cotyledons are considerably wider than thick, and the axis of the embryo is rotated so that the cotyledons lie parallel to the surface.

EXTERNAL CHARACTERISTICS

The seeds of this family are mostly elongate and are roughly elliptic in outline. In various species, as *Plantago lanceolata,* they are characteristically strongly boat-shaped with thick incurved margins; others (e. g., *P. virginica)* are somewhat bowl-like, the ventral surface much less scooped out; contrariwise, both surfaces of such forms as *P. rugellii* are convex. The elliptic outline of the seeds is commonly distinct but in *P. major, P. rugellii* and related species it is almost completely obscured by irregular marginal truncations; the seeds thus appear abruptly blunt, pointed, several sided or angled.

The hilum is more or less medial on the ventral face and is relatively large, frequently conspicuous, and white margined. It occasionally appears divided into two hilum-like areas.

The seed coat is usually dull in appearance, finely punctate, striate or rugose, sometimes almost completely smooth and shining. The color varies from blackish or brown to dull red.

ASSOCIATED STRUCTURES

The fruit is a two-celled, two to several-seeded capsule which is dehiscent by an apical lid. Certain species typically bear only two seeds, i. e., one seed in each cell; these are mostly the forms in which the seeds are strongly boat-shaped. Other species generally mature several seeds in each cell of the capsule. Among these, the numerous ovules develop in close proximity to one another, and the ultimate shape of each individual seed is somewhat dependent upon its position relative to the others (i. e., *P. major* or *P. rugellii).*

Inasmuch as the seeds readily escape from the capsules at maturity, they are most commonly not observed in association with them.

CLASSIFICATION BY SEED CHARACTERS

Although the Plantaginaceae exhibit a variety of seed forms, these intergrade with one another to such an extent that, with the exception of certain common species, accurate classification by seed characters may present considerable difficulties.

COMPOSITAE

(Plate 10)

GENERAL CHARACTERISTICS

Seed (achene) longitudinally elongate from a basal attachment, straight or somewhat curved; terete, angled or much flattened; smooth or variously roughened or ribbed; commonly with an apical cluster of fine bristles or scales (the pappus). Embryo straight, filling entire cavity of seed. Endosperm reduced to a very thin layer, commonly appearing absent. Cotyledons large, lying flatwise against one another; radicle and hypocotyl short; plumule inevident.

MORPHOLOGY

Ovule anatropous, basal, solitary within the inferior ovary. Integument one, at maturity much reduced or absent, the seed becoming closely associated with the non-dehiscent pericarp. The seed of common usage is thus a one-seeded fruit, variously known as an achene or cypsella.

The pericarp is extremely diverse in nature, frequently of several distinct layers, the external portion commonly thick, sclerenchymatous or corky-ribbed. The seed coat is commonly completely absent or in other cases represented by a portion of the epidermis. The endosperm usually consists of one to two rows of partially crushed cells external to the embryo. The embryo is longitudinally placed; the cotyledons are large and lie flatwise against one another; radicle and hypocotyl short; plumule inevident.

EXTERNAL CHARACTERISTICS

As might be expected from the great number and diversity of the members of this family, the seeds are correspondingly variable. They are nearly always longitudinally elongate, may be straight, slightly curved, or more rarely strongly curved. An obconic form with the apex or with both ends truncate is quite common. In cross section the seeds are perhaps most commonly irregularly polygonal to slightly or strongly compressed.

Surface markings are, characteristically, in the form of longitudinal ribs, furrows or wings. These may be small, very thin, or large and conspicuous, frequently corky thickened. In many genera, however, the surface is without longitudinal markings,

in which case it is usually smooth, finely roughened or wrinkled. Reticulate, pitted or laterally ribbed surfaces are rather uncommon.

Among various superficial appendages, the pappus, more than any other seed character, is a structure characteristic of the Compositae. Said to be the remnants of the calyx, it arises from a somewhat raised crown about the depresssed style base and may consist of numerous fine bristles, stiff awns, barbs or scales; in a few cases it is entirely absent.

Other external structures include hairs, e. g., found in some species of *Bidens, Senecio, Erigeron, Solidago, Aster,* or small barbs or bristles as in *Apargia, Hypochaeris, Taraxacum* and *Bidens.*

The color of the seeds most commonly varies from yellowish to brown, grey or black; frequently the surface is blotched with various combinations of these colors. Members of the chicory tribe frequently possess a reddish-brown color.

The hilum region at the base of the seed sometimes presents definite diagnostic characters. It is frequently depressed, may be straight or oblique, is occasionally strongly marked by an evident oblique notch *(Centaurea).*

In some genera *(Anthemis, Centaurea)* achenes of two types are produced in the same head, those developing from the central flowers having a different color and shape than those at the margin.

ASSOCIATED STRUCTURES

The inflorescence of this family is an involucrate head bearing numerous flowers on a common receptacle. The achenes at maturity separate from the head as individual units and are not further associated with any other structures of the inflorescence.

The principal exception to the above generalization is the ragweed tribe. In this group, the seeds in each head are few in number, usually one to four, and at maturity frequently remain within the more or less hardened involucre. In *Ambrosia* the achene is solitary within and closely associated with the involucre, this entire structure commonly being termed the seed. The genera *Iva, Franseria* and *Xanthium* usually bear two to four achenes in each involucre. These, when occurring as admixtures in commercial seed lots, are usually separated from their involucral coverings by the action of cleaning machinery.

CLASSIFICATION BASED ON SEED CHARACTERS

It does not appear currently practical to make a clear-cut diagnosis of the principal natural groups of the Compositae by seed characters. While the seeds of the various tribes exhibit certain trends in structural make-up, there are frequent deviations from the typical form. Keys, based upon seed characters,

to members of this family would probably have to be artificial and possess leads direct to genera or species.

The following summaries for some of the principal tribes will allow some notion of the structural types found in these groups:

Ambrosieae (Characteristic genera: *Ambrosia, Xanthium, Franseria, Iva.)* Seeds obovoid or flattened, usually with a thin unornamented pericarp, one to four in number in each involucre and frequently persistent within that structure. Involucre globose to elongate, commonly spiny or with hooked bristles, variously ribbed, reticulate or hairy.

Anthemideae (Characteristic genera: *Anthemis, Chrysanthemum, Achillea, Matricaria.)* Seeds (i. e., the achenes) mostly quadrangular or polygonal, occasionally flattened, strongly truncate at ends. Surface with few to several strong, frequently corky-thickened ribs, occasionally ribless and warty. A well-developed irregular and frequently thick apical crown is present, but pappus generally obsolete or absent. Style base usually strongly depressed below the crown.

Astereae (Characteristic genera: *Aster, Solidago, Erigeron, Chrysopsis.)* Seeds generally small, oblong to obconic, not strongly truncate, in cross section elliptic to terete or angled. Surface most commonly wrinkled, ribbed or smooth, frequently hairy. Pappus of capillary bristles with the exception of a few genera such as *Boltonia, Bellis* and *Gutierrezia.* Style base not strongly depressed. Basal attachment region frequently a callus-like ring.

Cichorieae (Characteristic genera: *Cichorium, Sonchus, Lactuca, Taraxacum, Hieracium.)* A great diversity of form is exhibited by the seeds of members of this tribe. Perhaps the most characteristic shape is spindle-form, the achene apically being drawn out into a short, or in some cases (e. g., *Lactuca, Tragopogon)* a long, beak and tapering most sharply at the base. In *Cichorium* the seeds are abruptly truncate apically. Cross-sectional forms range from irregularly compressed to rounded. The seeds of many species of *Lactuca* appear strongly laterally flattened; this is due to the presence of wide, corky wings. The surface is characteristically longitudinally ribbed; the ribs sometimes possess tubercles or papillae which may be extended into short barbs as in *Taraxacum.* The pappus is generally represented by numerous, simple, barbed or plumose, capillary bristles but may be reduced to one to two rows of scales as in *Cichorium* or may be absent *(Lapsana).*

Cynarieae (Characteristic genera: *Cirsium, Arctium, Centaurea, Cnicus.)* Seeds straight or somewhat curved longitudinally, usually tapering at base (strongly notched basally in many species of *Centaurea),* tapering or truncate at apex. In lateral view they may be irregularly flattened, several sided or

sometimes plano-convex. The surface is usually smooth, finely roughened or scaly, but is strongly longitudinally ribbed in *Cnicus*. Color dull yellow to blackish, frequently with blotches of several shades of pigmentation. Pappus usually of capillary bristles arising from a distinct apical crown or flange, frequently deciduous at maturity. Style base commonly strongly depressed.

Eupatorieae (Characteristic genera: *Eupatorium, Ageratum, Brickellia, Mikania.)* Achenes oblong, mostly flattened-quadrangular in cross section, closely 6- to 15-ribbed, commonly black in color, sometimes glandular. Pappus mostly of bristles, sometimes of scales, rarely absent.

Helenieae (Characteristic genera: *Helenium, Gaillardia, Hymenopappus.)* Seeds mostly obconic, truncate at apex, terete or somewhat flattened. Surface smooth, irregularly fluted or angled, sometimes ribbed, commonly hairy. Attachment area frequently callus-like. Pappus usually present, of scales which are commonly awn-tipped or of bristles.

Helianthеae (Characteristic genera: *Helianthus, Rudbeckia, Bidens, Silphium.)* A great variety of shapes is exhibited by seeds of this tribe. A very common form is characteristic of those which are broadly oblong, straight or slightly curved, usually with the greatest width at the rounded-truncate apex. The faces are frequently concave. In cross section the seeds are usually somewhat compressed, may be elliptic or irregularly several sided. The general appearance of these structures, very similar to many of the Cynareae, can be exemplified by species of *Helianthus, Inula, Madia* and some representatives of *Rudbeckia.* Seeds of other members of this tribe are broadly oblong, quadrangular, frequently brick-like and truncate at both ends, e. g., species of *Brauneria, Rudbeckia* and *Heliopsis.* Seeds of yet other genera are strongly laterally compressed and broadly winged; characteristic among these are some of the species of *Bidens, Verbesina* and *Silphium.*

The most common surface markings are fine longitudinal striations, cross wrinkles, furrows or irregular cellular roughening. Some genera characteristically possess longitudinal ribs or nerves, but these are in the minority.

The scar occasionally forms a basal notch.

The pappus is usually not conspicuous, most commonly being of scales or forming an irregular crown about the apex of the seed. Sometimes it is of short awns or bristles, in the case of *Bidens* forming conspicuous stiff, barbed awns.

Inuleae (Characteristic genera: *Gnaphalium, Anaphalis, Antennaria, Pluchea.)* Seeds small, rectangular, tapering at ends. Surface faintly ribbed or entirely smooth. Scar region callus-like. Apex a distinct collar or ring. Pappus present, of numerous bristles, frequently easily deciduous.

Senecioneae (Characteristic genera: *Arnica, Erechtites, Senecio, Tetradymia.)* Seeds oblong, terete to quadrangular, usually truncate at both base and apex and commonly with a ring-like callus at both ends. Surface longitudinally ribbed. Pappus of capillary bristles.

Vernonieae (Characteristic genera: *Vernonia, Elephantopus.)* Seeds mostly cylindric, corky-ribbed (rarely without ribs), usually dark in color and commonly glandular. Pappus of stiff bristles.

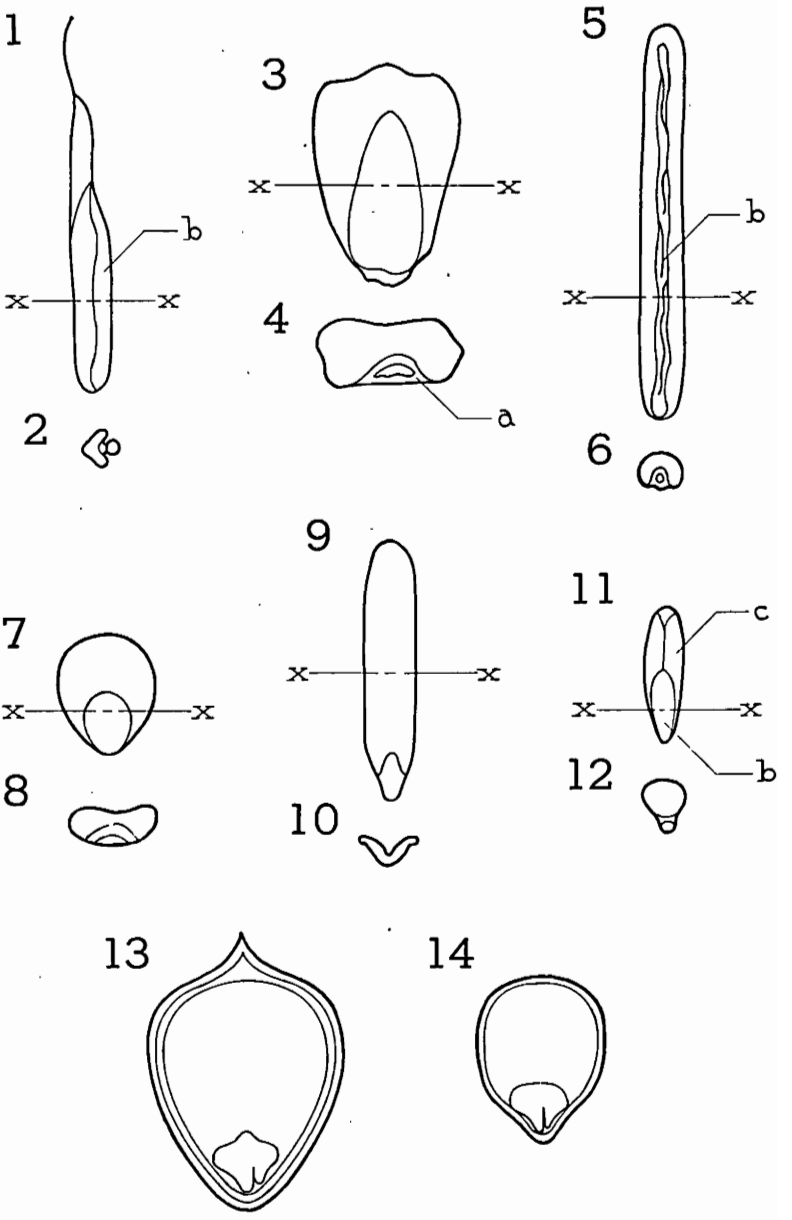

PLATE 1. GRAMINEAE, CYPERACEAE

Spartina michauxiana Hitchc.: 1. Longitudinal view X5. 2. Cross section X5. *Zea mays* L.: 3. Longitudinal view X2. 4. Cross section X2. *Zizania aquatica* L.: 5. Longitudinal view X3. 6. Cross section X3. *Paspalum floridanum* Michx.: 7. Longitudinal view X5. 8. Cross section X5. *Bromus secalinus* L.: 9. Longitudinal view X5. 10. Cross section X5. *Chloris gayana* Kunth.: 11. Longitudinal view X10. 12. Cross section X10. *Scirpus paludosus* A. Nels.: 13. Section parallel to face X10. *Carex vulpinoidea* Michx.: 14. Section parallel to face X10.
a. Scutellum. b. Embryo. c. Endosperm region. x-x. Plane of cross section.

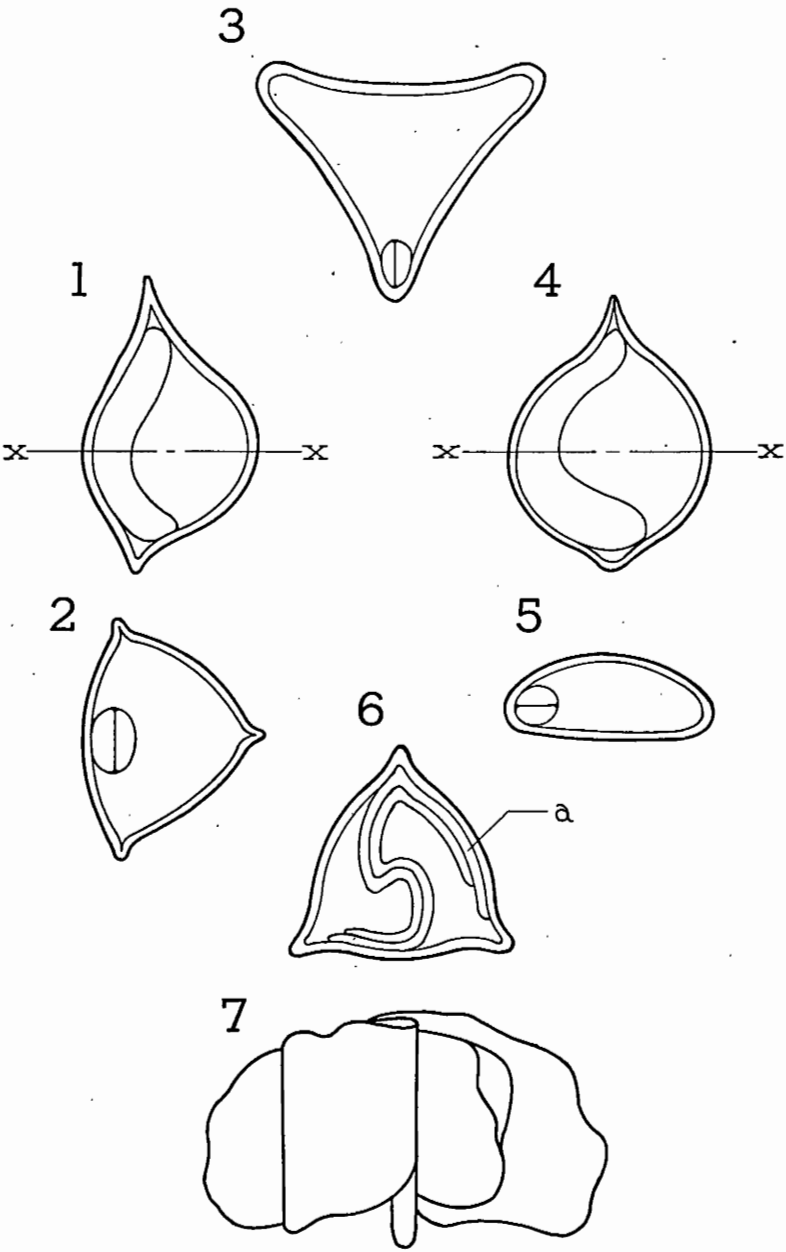

PLATE 2. POLYGONACEAE

Rumex crispus L.: 1. Longitudinal section X10. 2. Cross section X10. *Polygonum convolvulus* L.: 3. Cross section X10. *Polygonum persicaria* L.: 4. Longitudinal section X10. 5. Cross section X10. *Fagopyrum esculentum* Gaertn.: 6. Cross section X5. 7. Excised embryo X2½.
a. Cotyledon. x-x. Plane of cross section.

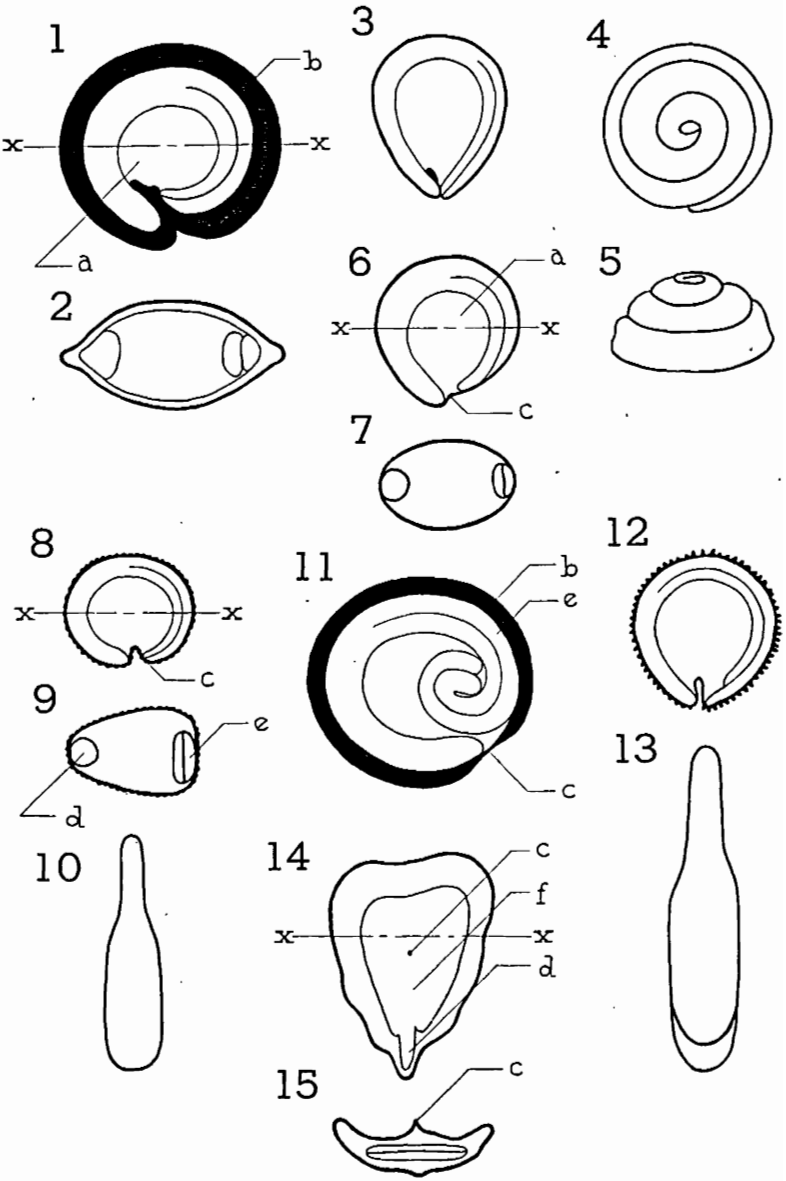

PLATE 3. CHENOPODIACEAE, AMARANTHACEAE, CARYOPHYLLACEAE

Chenopodium hydridum L.: 1. Section parallel to face X10. 2. Cross section X10. *Axyris amarantoides* L.: 3. Section parallel to face X10. *Salsola kali* L.: 4. Embryo, top view X10. 5. Embryo, side view X10. *Amaranthus blitoides* Wats.: 6. Section parallel to face X10. 7. Cross section X10. *Silene noctiflora* L.: 8. Section parallel to face X10. 9. Cross section X10. 10. Excised embryo, straightened out X10. *Spergula arvensis* L.: 11. Section parallel to face X10. *Agrostemma githago* L.: 12. Section parallel to face X10. 13. Excised embryo, straightened out X10. *Dianthus barbatus* L.: 14. Section parallel to face X10. 15. Cross section X10.

a. Perisperm. b. Wing. c. Hilum region. d. Radicle. e. Cotyledon. f. Embryo. x-x. Plane of cross section.

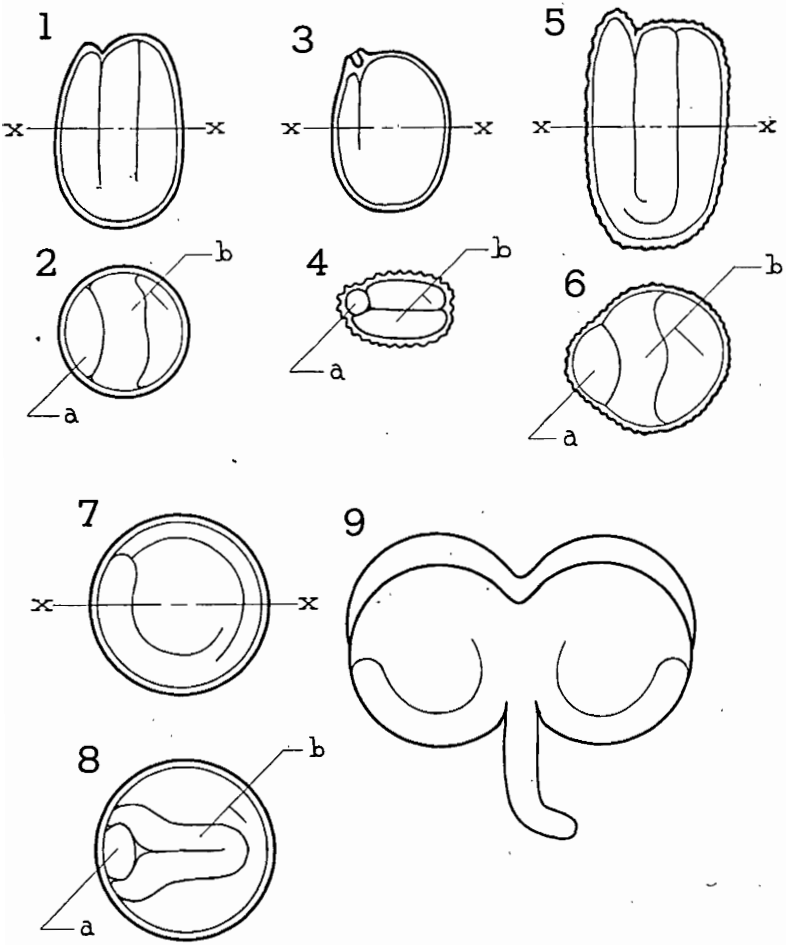

PLATE 4. CRUCIFERAE

Sisymbrium altissimum L.: 1. Longitudinal section X5. 2. Cross section X5. *Thlaspi arvense* L.: 3. Longitudinal section X5. 4. Cross section X5. *Conringia orientalis* Dumont.: 5. Longitudinal section X5. 6. Cross section X5. *Brassica napus* L.: 7. Medial section X10. 8. Cross section X10. 9. Excised embryo X10. a. Radicle. b. Cotyledons. x-x. Plane of cross section.

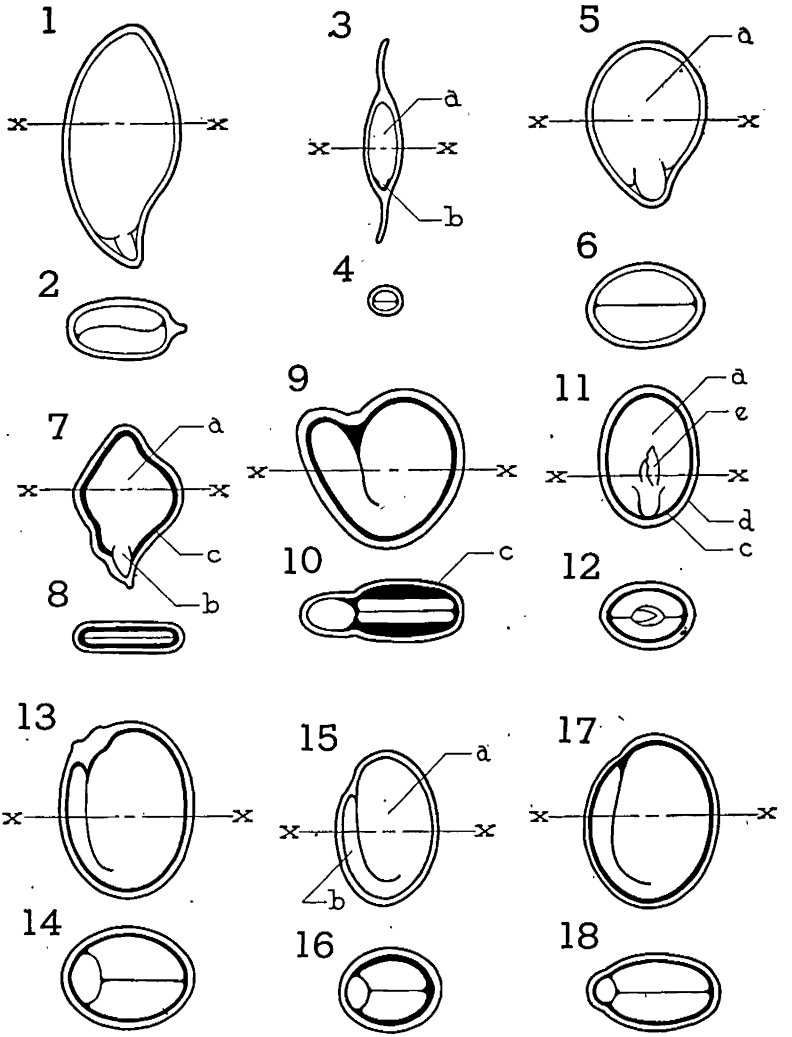

PLATE 5. ROSACEAE, LEGUMINOSAE

Sorbus americana Marsh.: 1. Longitudinal section X10. 2. Cross section X10. *Spiraea spp.*: 3. Longitudinal section X10. 4. Cross section X10. *Potentilla argentea* L.: 5. Longitudinal section X20. 6. Cross section X20. *Chamaecrista fasiculata* (Michx.) Greene: 7. Longitudinal section X5. 8. Cross section X5. *Astragalus canadensis* L.: 9. Longitudinal section X10. 10. Cross section X10. *Acacia melanoxylon* R. Br.: 11. Longitudinal section X5. 12. Cross section X5. *Lupinus albifrons* Benth.: 13. Longitudinal section X5. 14. Cross section X5. *Trifolium incarnatum* L.: 15. Longitudinal section X10. 16. Cross section X10. *Lespedeza stipulacea* Maxim.: 17. Longitudinal section X10. 18. Cross section X10. a. Cotyledon. b. Radicle. c. Endosperm. d. Seed coat. e. Plumule. x-x. Plane of cross section.

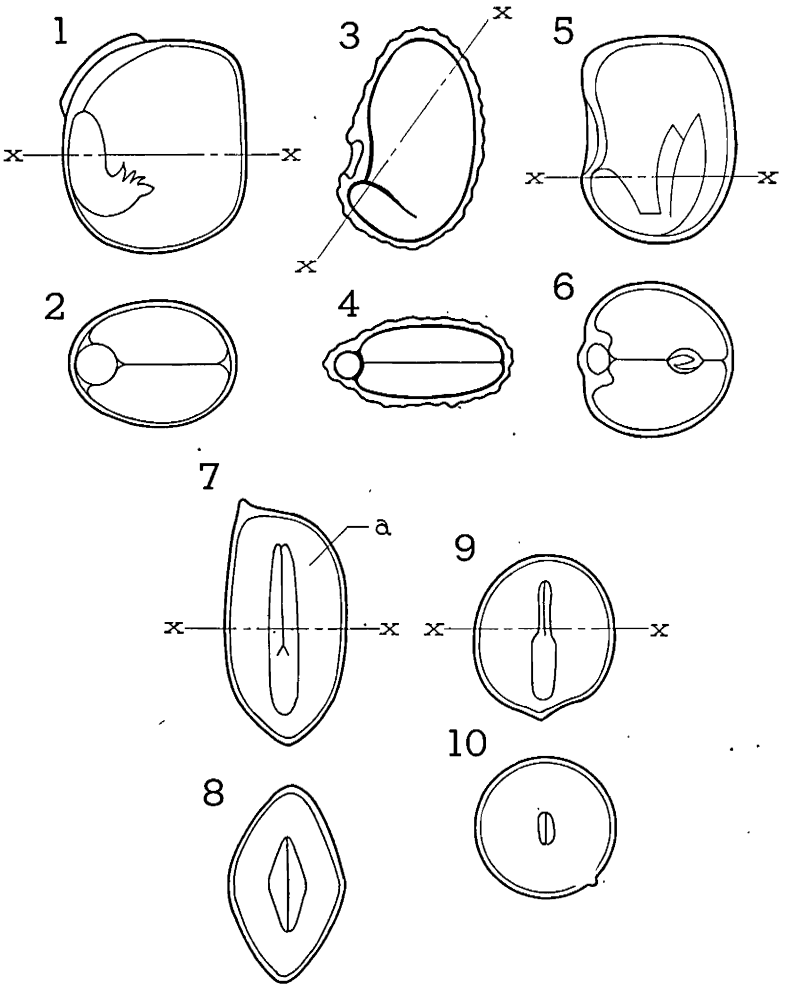

PLATE 6. LEGUMINOSAE, EUPHORBIACEAE

Vicia atropurpurea Desf.: 1. Longitudinal section X5. 2. Cross section X5. *Baptisia leucantha* T. & G.: 3. Longitudinal section X5. 4. Cross section X5. *Phaseolus spp.:* 5. Longitudinal section X5. 6. Cross section X5. *Croton glandulosus* L.: 7. Longitudinal section X10. 8. Cross section X10. *Euphorbia cyparissias* L.: 9. Longitudinal section X10. 10. Cross section X10.
a. Endosperm. x-x. Plane of cross section.

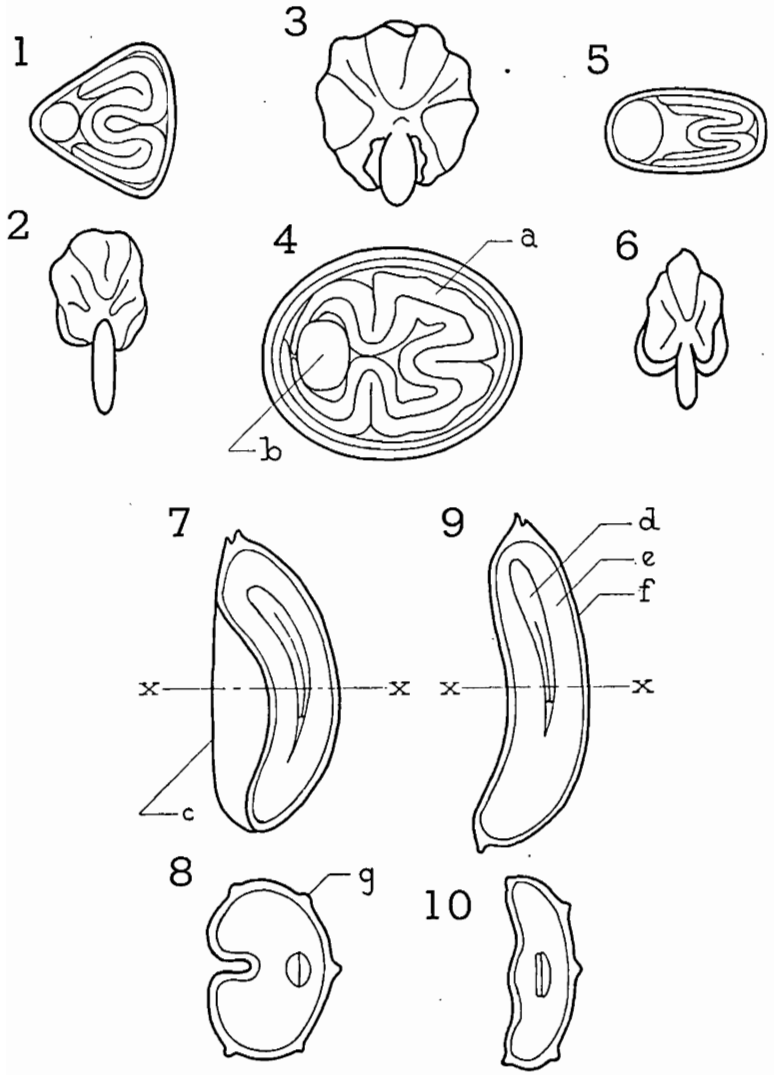

PLATE 7. MALVACEAE, UMBELLIFERAE

Sida spinosa L.: 1. Cross section X10. 2. Excised embryo X5. *Hibiscus esculentus* L.: 3. Excised embryo X2½. 4. Cross section X5. *Malva rotundifolia* L.: 5. Cross section X10. 6. Excised embryo X5. *Conium maculatum* L.: 7. Longitudinal section X10. 8. Cross section X10. *Pimpinella anisum* L.: 9. Longitudinal section X10. 10. Cross section X10.

a. Cotyledon. b. Radicle. c. Ventral margin of mericarp. d. Embryo. e. Endosperm. f. Pericarp. g. Rib. x-x. Plane of cross section.

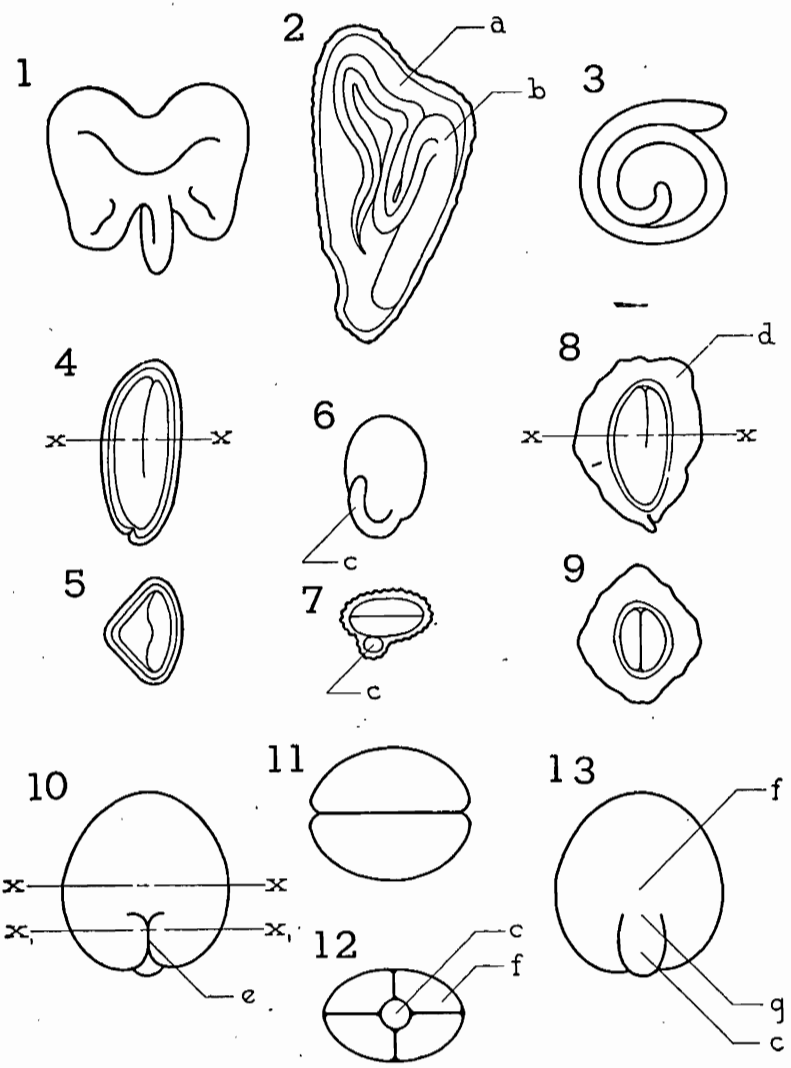

PLATE 8. CONVOLVULACEAE, LABIATAE

Ipomoea spp.: 1. Excised, straightened embryo X2½. 2. Longitudinal section X10. *Cuscuta spp.:* 3. Excised embryo X20. *Dracocephalum parviflorum* Nutt.: 4. Longitudinal section X10. 5. Cross section X10. *Scutellaria lateriflora* L.: 6. Excised embryo X10. 7. Cross section (of seed) X10. *Teucrium canadense* L.: 8. Longitudinal section X10. 9. Cross section X10. *Perilla frutescens* (L.) Britt.: 10. Excised embryo X10. 11. Cross section of embryo (x-x) X10. 12. Cross section of embryo (x_1-x_1) X10. 13. Longitudinal section of embryo X10.

a. Endosperm. b. Embryo. c. Radicle. d. Pericarp. e. Cotyledonary slit. f. Cotyledon. g. Hypocotyl. x-x. Plane of cross section.

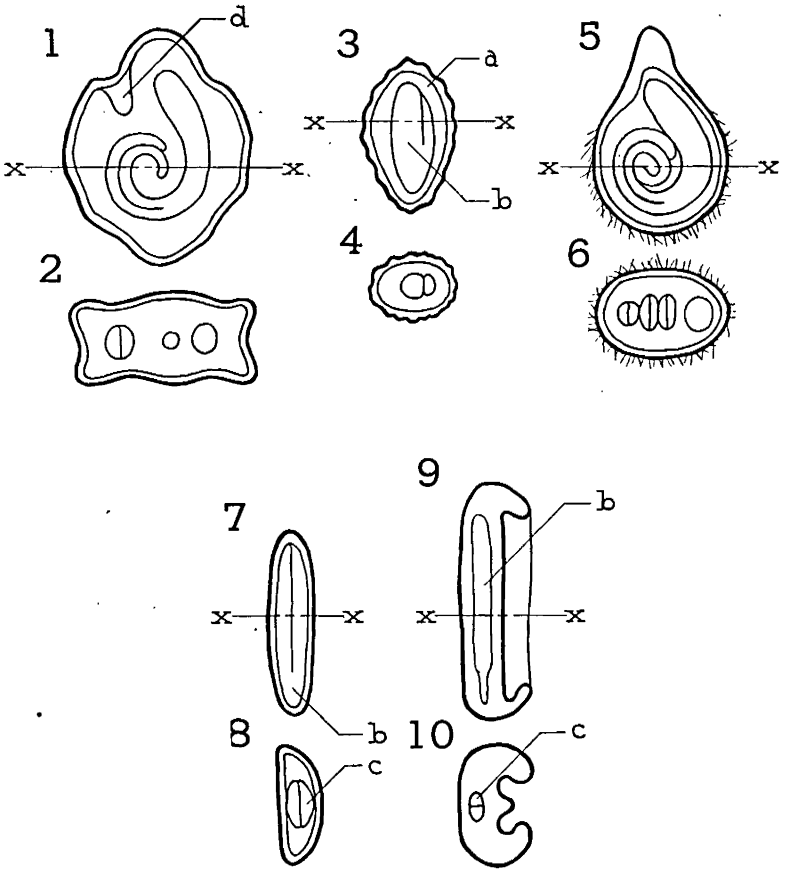

PLATE 9. SOLANACEAE AND PLANTAGINACEAE

Solanum rostratum Dunal.: 1. Section parallel to face X10. 2. Cross section X10. *Nicotiana tabacum* L.: 3. Longitudinal section X20. 4. Cross section X20. *Lycopersicon esculentum* Mill.: 5. Section parallel to face X10. 6. Cross section X10. *Plantago rugellii* Dene.: 7. Longitudinal section X10. 8. Cross section X10. *Plantago lanceolata* L.: 9. Longitudinal section X10. 10. Cross section X10.
a. Endosperm. b. Embryo. c. Cotyledon. d. Hilar slit. x-x. Plane of cross section.

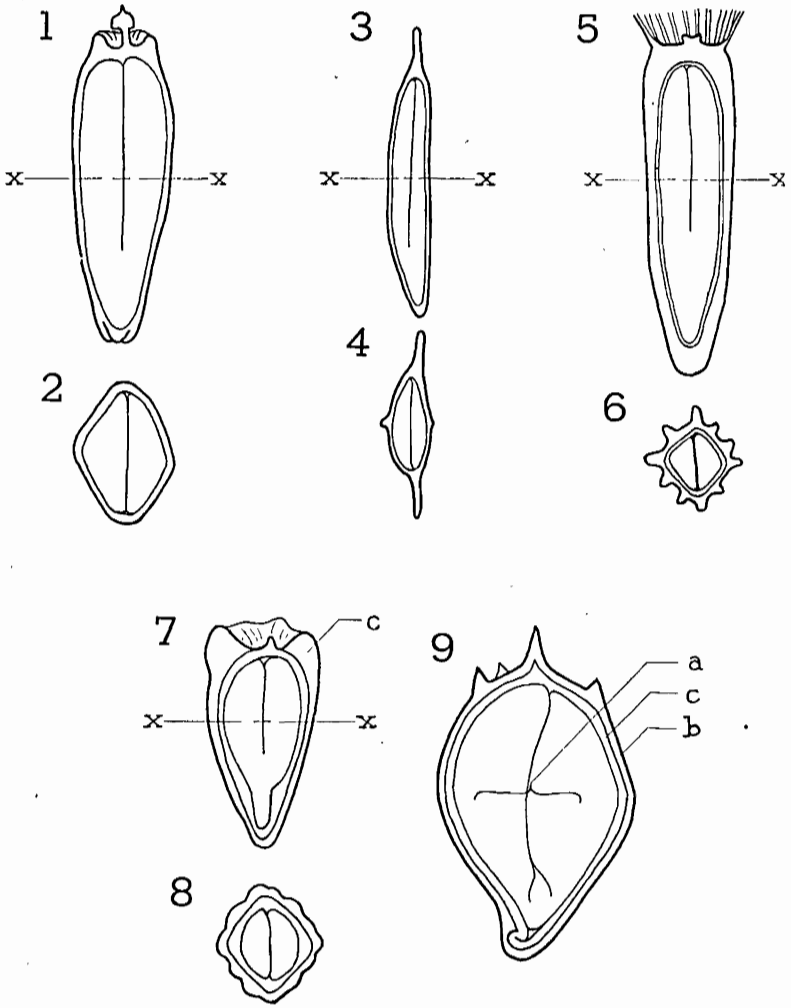

PLATE 10. COMPOSITAE

Cirsium lanceolatum Hill: 1. Longitudinal section X5. 2. Cross section X5. *Lactuca scariola* L.: 3. Longitudinal section X10. 4. Cross section X10. *Vernonia fasiculata* Michx.: 5. Longitudinal section X10. 6. Cross section X10. *Anthemis arvensis* L.: 7. Longitudinal section X10. 8. Cross section X10. *Ambrosia elatior* L.: 9. Longitudinal section X10.

a. Embryo. b. Involucre. c. Pericarp. x-x. Plane of cross section.

LITERATURE

(1) Artschwager, Ernst. Development of flowers and seed in the sugar beet. Jour. Agr. Res. 34:1-25. 1927.

(2) Beetle, Alan A. A key to the North American species of the genus *Scirpus* based on achene characters. Amer. Midl. Nat. 29:533-538. 1943.

(3) Blake, Anita Mary. Akenes of some Compositae. North Dakota Agr. Coll. Bul. 218. 1928.

(4) Gale, Shirley. *Rhynchospora*, section Eurhynchospora, in Canada, the United States and the West Indies. Rhodora 46:89-134, 159-197, 207-249, 255-278. 1944.

(5) Hayward, Herman E. The structure of economic plants. The Macmillan Co., New York. 1938.

(6) Hillman, F. H. Testing farm seeds in the home and in the rural school. U. S. Dept. Agr. Farmers' Bul. 428. 1911.

(7) ———— and Henry, Helen H. Photographs of drawings of seeds. U. S. Dept. Agr. Div. of Seed Investigation. Rev. 1935.

(8) Hitchcock, A. S. Manual of the grasses of the United States. U. S. Dept. Agr. Misc. Publ. 200. 1935.

(9) Johnson, A. M. Taxonomy of the flowering plants. The Century Co., New York. 1931.

(10) Korsmo, Emil. Weed seeds. Gyldendal Norskforlag, Oslo. 1935.

(11) Mackenzie, K. K. North American Cariceae 2 v. The New York Botanical Garden, New York. 1941.

(12) McGivney, Sister M. Vincent de Paul. A revision of the subgenus Eucyperus found in the United States. Catholic Univ. Amer. Publ. Biological Series No. 26. 1938.

(13) Murley, Margaret. A seed key to fourteen species of Geraniaceae. Proc. Iowa Acad. Sci. 51:241-246. 1944.

(14) ———— Distribution of Euphorbiaceae in Iowa with seed keys. Iowa State College Jour. Sci. 19:415-427. 1945.

(15) ———— Umbelliferae in Iowa with seed keys. *Ibid.* 20:349-364. 1946.

(16) Musil, Albina F. Seeds of commercial species of *Brassica*. Proc. A.O.S.A. 34:132-138. 1942.

(17) ————Distinguishing characters of the seeds of 4 species of *Agropyron*. *Ibid.* 34:124-131. 1942.

(18) ————Testing farm seeds in home and school. U. S. Dept. Agr. Misc. Publ. 437. 1942.

(19) ————Seeds of grasses cultivated for forage or occurring incidentally with crop seeds: the genus *Setaria*. U. S. Dept. Agr. Div. Forage Crops and Diseases. 1944.

(20) ————Seeds of grasses cultivated for forage or occurring incidentally with crop seeds: the genus *Panicum*. *Ibid.* 1944.

(21) ————Seeds of dodder occurring with crop seeds. *Ibid.* 1944.

(22) ————Distinguishing species of *Poa* from their seed. *Ibid.* 1946.

(23) ————Distinguishing species of *Avena* from their seed. *Ibid.* 1946.

(24) Netolitsky, Fritz. Anatomie der Angiospermen-Samen. In: Linsbauer, Handbuch der Pflanzen Anatomie. II:2 Band 10. 1926.

(25) Pammel, L. H. Anatomical characters of the seeds of Leguminosae chiefly genera of Gray's Manual. Trans. Acad. Sci. St. Louis 9:91-263. 1899.

(26) Pax, F. and Hoffman, K. Caryophyllaceae. In: Engler & Prantl. Die naturlichen Pflanzenfamilien. ed. 2, 16c.:275-367. 1934.

(27) Pilger, Robert. Plantaginaceae. In: Engler. Das Pflanzenreich. Vol. 102. 1937.

(28) Porter, R. H. Testing the quality of seeds for farm and garden. Iowa Agr. Exp. Sta. Res. Bul. 334:495-586. 1944.

(29) Reeves, R. G. Comparative anatomy of the seeds of cottons and other malvaceous plants. I. Malveae and Ureneae. Amer. Jour. Bot. 23:291-296. 1936.

(30) ————Comparative anatomy of the seeds of cottons and other malvaceous plants. II. Hibisceae. *Ibid.* 23:394-405. 1936.

(31) Robinson, B. L. and Fernald, M. L. Gray's New Manual of Botany. 7th ed. American Book Co., N. Y. 1908.

(32) Schneider, Margarete. Untersuchungen uber die Embryobildung und Entwicklung der Cyperaceen. Bot. Centbl. Beih. Abt. 1, 49:649-674. 1932.

(33) Schuman, K. Malvaceae. In: Engler and Prantl. Die naturlichen Pflanzenfamilien **III-6**:30-53. 1896.

(34) Simpson, D. M., Adams, Caroline L. and Stone, G. M. Anatomical structure of the cottonseed coat as related to problems of germination. U. S. Dept. Agr. Tech. Bul. 734. 1940.

(35) Svenson, H. K. Monographic studies in the genus *Eleocharis*. Rhodora: 31:121-135, 152-163, 167-191, 199-219, 224-242, 1929. 34:193-203, 215-227, 1932. 36:377-389, 1934. 39:210-231, 1937. 41:1-19, 43-77, 1939.

(36) Wettstein, Richard. Solonaceae. In: Engler and Prantl. Die naturlichen Pflanzenfamilien **IV-3b**:4-38. 1891.

(37) ————Handbuch der Systematischen Botanik. 4th ed. F. Deuticke, Leipzig und Wien. 1935.

(38) Wheeler, L. C. *Euphorbia*, subgenus Chamaesyce in Canada and the U. S. Rhodora 43:97-154, 168-205, 223-286. 1941.

(39) Wilczek, Ernst. Beitrage zur Kentniss des Baues der Frucht und des Samens der Cyperaceen. Bot. Centralb. 51:129-138, 193-201, 257-265. 1892.

(40) Woodcock, E. F. The structure of the mature seed of *Eriogonum microthecum*. Ann. Report of Mich Acad. Sci. 20:233-235. 1918.

(41) ————Morphological studies of *Alsine media*. Pap. Mich. Acad. Sci. Arts and Letters. 6:379-402. 1926.

(42) ————Observations on the morphology of the seed of *Cerostium vulgatum*. *Ibid.* 8:233-238. 1927.

(43) ————Seed development in *Amaranthus caudatus* L. *Ibid.* 15:173-178. 1931.